POSTFIRE RECRUITMENT IN FLORIDA SAND PINE SCRUB IN COMPARISON WITH CALIFORNIA CHAPARRAL

By

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POSTFIRE RECRUITMENT IN FLORIDA SAND PINE SCRUB IN COMPARISON WITH CALIFORNIA CHAPARRAL

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The role of fire as a disturbance in communities can be characterized by the collective postfire recruitment traits of species. In communities with large proportions of species recruiting via postfire seedling establishment (e.g., Mediterranean-climate communities), fires are essential for maintaining plant species composition.

This study evaluated the role of fire in Florida sand pine scrub by characterizing postfire recruitment compared to primarily Mediterranean-climate communities. The influence of fire on seed survival and seedling microsites was quantified in two experimentally burned sand pine scrub sites, and postfire recruitment was characterized at community and species levels.

Seed survival through fires was more likely below the soil surface than at the soil surface, as determined by temperature measurements during fires, postfire recovery of seeds placed in the sites to be burned, and laboratory seed germination experiments. Fires reduced litter depths and increased canopy openness in potential seedling microsites. Experiments on seedling emergence from microsites simulating pre- and postfire conditions demonstrated that seedling emergence was water-limited during both summer and winter, but high soil temperatures contributed to harsh conditions for seedling establishment during summer.

Postfire seedling recruitment was less prevalent in Florida sand pine scrub than in Mediterranean-climate communities; relatively low values were observed for sand pine scrub postfire seedling density, soil seed bank density, and proportion of species with postfire seedling establishment. Three of five focal species had strong seedling establishment responses after the experimental fires.

Comparisons of postfire seedling recruitment patterns in relation to site characteristics among Florida communities and among southern California communities showed that postfire seedling recruitment in Florida was more prevalent in soils with relatively harsh conditions for seedling establishment. Seedling densities in California, however, were higher in soils providing relatively mesic conditions for seedling establishment.

Although the effects of fire on seed survival and microsite conditions in Florida sand pine scrub appear similar to those in other fire-influenced communities, postfire recruitment is relatively "uncoupled" from fire compared to recruitment in Mediterranean-climate communities. Different underlying processes may influence patterns of postfire recruitment in Florida and southern California.

CHAPTER 1

GENERAL INTRODUCTION

Fire occurs as a disturbance in virtually all ecosystems on earth (Whelan 1995). Fire frequency, intensity, season and type vary among ecosystems, and consequently effects of fires as disturbances on ecosystems vary widely. As a general rule, however, fires top-kill or completely kill individuals of some plant species, and these species must rely on either postfire regrowth or establishment to persist in burned sites.

Two general modes by which plant species recover after fires are resprouting and seedling establishment. Various combinations of these modes are associated with different plant species life history strategies. Plants resprout after fires from buds on roots or belowground stems, or from epicormic buds (Keeley 1981). "Obligate resprouters" are capable of only resprouting after fires, while "facultative resprouters" resprout and establish seedlings (Naveh 1975). Although some taxa have highly developed epicormic bud-containing structures (i.e., lignotubers, burls) that facilitate postfire resprouting (James 1984), resprouting is often not considered a specific adaptation to fire (Wells 1969, Axelrod 1989).

In addition to obligate and facultative resprouters, "obligate seeders" (Naveh 1975) are incapable of resprouting after being top-killed by fires, and recruit after fires only by establishing seedlings. These species often have life history traits that are considered specific adaptations to fire, such as serotiny and heat- or smoke-induced germination (e.g., Wells 1969, Gill 1981, Barbour and Minnich 1990, Le Maitre and Midgley 1992).

The collective postfire recruitment traits of species may largely define the effect of fire as a disturbance on a community. For example, in communities in which a large proportion of the species are obligate resprouters (e.g., some grasslands), fires consume aboveground biomass and influence community physiognomy, but do not appreciably influence plant species turnover rates (Wright and Bailey 1982). In contrast, in communities in which a large proportion of the species are obligate seeders and facultative resprouters (e.g, Mediterranean-climate ecosystems), postfire seedling recruitment is relatively important at the community level, and fires are often essential for maintaining plant species diversity (Christensen 1985).

Community-level postfire recruitment characteristics are influenced by several factors. Evolutionary histories and phylogenetic constraints on species in the community initially determine the potential for postfire seedling recruitment (Peet 1978, Herrera 1992). Community-level recruitment characteristics are further influenced, however, by the fire regime (e.g., fire frequency, intensity and season) and by abiotic conditions (e.g., rainfall abundance and seasonal pattern, soil texture and nutrient status). Thus, given the phylogenetic constraints of species, community-level postfire recruitment characteristics reflect the role of fire within the abiotic environment in a community.

The objective of this research was to characterize postfire recruitment in Florida sand pine scrub, and to evaluate the role of fire as a disturbance in sand pine scrub in comparison with other fire-influenced ecosystems. Sand pine scrub is a shrub-dominated community that occurs primarily in Florida on well-drained, sandy, nutrient-poor soils. One of several types of Florida scrub dominated by obligately-resprouting oak species (Quercus spp.) and sparse in herbaceous species, sand pine scrub is distinguished by a preponderance of obligately-seeding sand pine (Pinus clausa) in the overstory.

Two types of sand pine scrub are generally recognized--inland peninsular sand pine scrub, that occurs along the central peninsular ridge of Florida on Miocene to early Pleistocene paleodunes; and coastal sand pine scrub, that occurs on more recent coastal dunes formed during the Pleistocene (Myers 1990). Natural disturbance regime and sand pine life history characteristics differ between these two types of sand pine scrub. Fire is the predominant natural disturbance in inland peninsular scrub; sand pines in this type of scrub, sometimes recognized as a distinct variety (*Pinus clausa* var. *clausa*), have serotinous cones that open after exposed to heat from a fire. In contrast, in coastal sand pine scrub hurricanes are more prevalent than fires as natural disturbances. Sand pines in coastal scrub, sometimes designated as *Pinus clausa* var. *immuginata*, generally have non-serotinous cones (Ward 1963, Myers 1990). Nomenclature follows Wunderlin (1982) unless otherwise noted.

I conducted the research for this study in inland peninsular sand pine scrub. As in other fire-influenced communities in Florida, lightning-ignited natural fires occur during late spring to late summer. Fires are most prevalent and extensive, however, during April through early June, when high lightning frequencies often coincide with periods of drought (Komarek 1964, Myers 1990). Fires are intense and infrequent, occurring every 10 to 100 years on a given site (Myers 1990).

Although community-level postfire recruitment has been characterized for rosemary scrub, scrubby flatwoods and oak-saw palmetto scrub (Abrahamson 1984*a*, 1984*b*, Schmalzer and Hinkle 1992), little research has been conducted in sand pine scrub as defined in this study, and mechanisms associated with postfire recruitment have rarely been addressed. A community-level study conducted in sand pine scrub at Ocala National Forest reported higher species richness and diversity of nonwoody plants six years after burning and salvage logging than in mature forest; some of this difference, however, may have been in response to disturbance caused by logging (Greenberg et al. 1995). Although postfire recruitment characteristics have been quantified for a number of Florida scrub plant species (Johnson 1982, Abrahamson 1984b, Minno 1987, Hartnett and Richardson 1989, Menges 1992, Menges and Kohfeldt 1995, Abrahamson and Abrahamson 1996b), life history characteristics remain unknown for a large proportion of relatively inconspicuous sand pine scrub species.

I collected much of the data used to characterize postfire recruitment in Florida sand pine scrub before, during and after experimental fires conducted at Ocala National Forest and Archbold Biological Station, Florida during May 1993. I quantified abiotic conditions relevant to seed survival, seed germination and seedling establishment; and quantified postfire recruitment characteristics at species and community levels.

Abiotic conditions quantified included litter depths and percent open canopy values before and after the experimental fires in potential microsites for seedlings, and soil temperatures during the fires in potential microsites for seeds. Postfire recruitment characteristics (e.g., prevalence of postfire resprouting, seedling densities before and after fires) were quantified for Calamintha ashei (Weatherby) Shinners (Lamiaceae), *Chapmannia floridana* Torr. and Gray (Fabaceae), *Eriogonum longifolium* var. *gnaphifolium* Gandoger (Polygonaceae; Reveal 1981), *Garberia heterophylla* (Bartr.) Merr. & Harp. (Asteraceae) and *Palafoxia feayi* A. Gray (Asteraceae), all small-statured (< 2 m tall) species relatively common in sand pine scrub. *Eriogonum longifolium* var. *gnaphifolium* and *Garberia heterophylla* seeds were used in two additional studies--one study quantified the effects of temperatures maintained during fires on seed survival, and the other study quantified the effects on seedling establishment of experimental microsites simulating pre- and postfire conditions.

To characterize postfire recruitment in sand pine scrub relative to recruitment in other fire-influenced communities, I applied a conceptual framework describing species-level recruitment in relation to disturbance to recruitment at the community level. Grubb (1988) characterized species-level recruitment as either "coupled" or "uncoupled" to disturbance episodes, with "coupled" recruitment occurring only after disturbances, and "uncoupled" recruitment occurring at other times relative to disturbances. In this dissertation I expand Grubb's characterization to community-level recruitment. At the community level, recruitment relative to disturbance likely cannot be characterized as strictly "coupled" or "uncoupled," but falls somewhere on a gradient between the two extremes.

Determining the relative positions of fire-influenced communities on a gradient from having "uncoupled" to "coupled" recruitment should help elucidate differences in community-level responses to fires. To characterize recruitment in sand pine scrub relative to other communities, I measured three specific response variables related to community-level recruitment:

1. postfire seedling density
2. proportion of species with postfire seedling establishment
3. density of seeds in soil seed bank.

Communities with "coupled" recruitment relative to other communities should have relatively high values for these variables. Conversely, communities with "uncoupled" recruitment should have relatively low values for the variables.

Seedling densities were estimated before and after the experimental sand pine scrub fires, and soil seed bank densities of several recently burned and mature sites were quantified; these data were compared with similar data from other fire-influenced communities. In addition, relative proportions of plant species in sand pine scrub with various growth forms and postfire recruitment traits were determined from data collected from aboveground vegetation and from seed banks. These data also were compared with similar data from other fire-influenced communities.

The research characterizing sand pine scrub postfire recruitment concluded with a study in which postfire recruitment characteristics (seedling densities, proportions of species represented by seedlings) and site characteristics (percent open canopy values, soil nutrient and textural properties) of sand pine scrub were compared with similar data collected in two other fire-influenced communities in Florida, and with data collected in three types of California chaparral. To suggest processes influencing postfire recruitment in different communities and at different spatial scales, I examined trends in seedling recruitment and site characteristics among communities both within and between the two geographic regions.

CHAPTER 2

POSTFIRE SEEDLING ESTABLISHMENT OF SMALL-STATURED PERENNIALS IN FLORIDA SAND PINE SCRUB

Introduction

Sand pine scrub is a fire-maintained community found primarily in Florida on well-drained, sandy, low-nutrient soils of former Miocene to Pleistocene sand dunes (Myers 1990). The community is dominated by several species of oaks (*Quercus* spp.), often with an overstory of sand pine (*Pinus clausa*). Herbaceous, partially woody, and small-statured (< 2 m tall) woody species are sparse. Natural fires in this community are lightning-ignited during late spring to late summer, and occur every 10 to 100 years on a given site (Myers 1990).

Postfire responses of the most abundant plant species in sand pine scrub have been documented. The oaks and most other large shrubs resprout and do not establish seedlings in response to fires, while sand pine and Florida rosemary (*Ceratiola ericoides*), a woody shrub, are killed by fire and establish seedlings afterwards (Johnson 1982, Abrahamson 1984*b*, Schmalzer and Hinkle 1987, Myers 1990, Menges and Kohfeldt 1995). Little information is available, in contrast, on the life histories and ecology of small-statured woody and herbaceous species. Many of these species are endemic to Florida scrub, and face threats to continued persistence due to habitat destruction and long-term fire suppression. Increased understanding of sand pine scrub community-level processes and plant species life history strategies in relation to fire should improve our ability to predict community responses to different disturbance regimes, and should lead to more effective conservation and management of remaining scrub patches.

Sand pine scrub shares some physiognomic and fire regime (e.g., fire frequency and intensity) characteristics with some more well-known pyrogenic communities in Mediterranean-type climates (Keeley and Keeley 1988, Myers 1990), and therefore might be expected to have similar species- and community-level responses to fires. But although variation in fire frequency and intensity may account for differences in species-level and community-level responses within geographic regions, this explanation does not seem to be generalizable across geographic regions. For example, although both California chaparral and sand pine scrub infrequently burn in intense fires, chaparral typically has a strong postfire flush of flowering and seedling establishment by herbaceous annual species (e.g., Christensen and Muller 1975), while this response has been rarely reported in sand pine scrub (Myers 1990).

Fire occurrence in ecosystems may be characterized by modal frequency, intensity, and time of year (Gill 1981), but these properties also are superimposed on abiotic conditions such as rainfall abundance and temporal pattern, as well as soil texture and nutrient status. Because such conditions commonly change over a geographic scale and, like fire, can exert strong selective pressures on plant life history characteristics, abiotic conditions should be included in a conceptual framework to predict vegetative responses to fire across geographic regions.

A conceptual framework for species-level recruitment proposed by Grubb (1988) seems applicable across geographic regions, and may help us to understand and predict Florida sand pine scrub vegetation responses to fire on the basis of known responses in other pyrogenic communities. Grubb characterized recruitment as either "coupled" or "uncoupled" to disturbance episodes, and presented some examples of plant species life history characteristics and abiotic ecosystem conditions associated with each recruitment pattern. According to his characterization, plant species recruitment in California chaparral as described above would be "coupled" with fire. Abiotic conditions in chaparral that may contribute to this pattern of recruitment include loamy or clayey soils with relatively good moisture-holding capacity, and cool, wet weather during winter and spring, when seedling establishment typically occurs.

Abiotic conditions in Florida sand pine scrub are different from those in chaparral. Soils are sandy and the weather immediately after most lightning-ignited fires is hot, causing high rates of evaporation from the soil surface. Since such conditions are harsh for seedling establishment soon after fires, recruitment in sand pine scrub is expected to be "uncoupled" from fire for a relatively high number of species.

Since (1) fire and abiotic conditions constitute strong selection pressures during plant species recruitment and (2) postfire recruitment at the community level is a composite of individual plant species recruitment responses, community-level responses to fire should vary across geographic regions with differences in prevailing abiotic conditions. I suggest that recruitment responses to fire may be characterized for pyrogenic communities in different geographic regions by quantifying numbers of species with recruitment "coupled" to fire occurrence relative to species with recruitment "uncoupled" to fires.

The purpose of this study was to describe the community-level recruitment response to fire in sand pine scrub, and to compare postfire recruitment in sand pine scrub to that in other pyrogenic communities. The study also involved quantifying postfire seedling establishment of several herbaceous and small-statured woody species in relation to fire-induced changes in microsite characteristics in sand pine scrub. Species chosen for study were relatively common at study sites, and were assumed to be representative of small-statured perennial species in the community. Measured properties and their expected patterns are listed below:

1. prefire and postfire microsite conditions relevant to seedling establishment- fire reduces litter depths and increases canopy openness, and homogenizes prefire spatial patterns of these variables;
2. magnitude of seedling establishment relative to prefire seedling density- postfire seedling densities are small compared to densities in other fire-prone communities;
3. postfire response characteristics of several small-statured perennial species- sand pine scrub species have a variety of postfire response characteristics (i.e., life history strategies), and species with "uncoupled" recruitment should be relatively well-represented in sand pine scrub.

Methods

Study Sites

The study was conducted at two sand pine scrub sites in peninsular Florida. The first site was a 9 ha tract located at Archbold Biological Station (hereafter "Archbold") in Highlands County (27° 15', 81° 15'). The site was last burned in 1927. Dominant vegetation consisted of *Quercus myrtifolia*, *Q. geminata*, *Q. chapmannia*, and several other woody shrubs, with an overstory of *Pinus elliottii* var. *densa* and *P. clausa*. Densities of *P. clausa* varied from 5 to 100 trees/ha.

The second site was an 86 ha area in Ocala National Forest (hereafter "Ocala") in Marion County (29° 08', 81° 45'), 175 km north of the Archbold site. The Ocala site last burned in 1935. Dominant shrub species were similar to those at Archbold, but *P. clausa* was much more dense (approximately 700 trees/ha; Outcalt and Greenberg unpublished data), and P. elliottii was absent from the overstory.

Soils at the two sites are almost entirely of the Astatula series. These soils are sandy with high permeability, and generally encompass flat to moderately sloping areas. Depth to the water table is over 2 m (USDA Soil Conservation Service 1975, 1989).

Prefire Data Collection

Five relatively common plant species were chosen for characterization of life history traits. Permanent 1 x 1 m plots were centered on nonrandomly located adult individuals of each species at the Archbold and Ocala burn sites and at a control site near each burn site. The study species included an herbaceous species, Eriogonum longifolium var. gnaphifolium (Polygonaceae; Reveal 1981); a suffrutescent species, Chapmannia floridana (Fabaceae); and three small-statured woody shrubs, Calamintha ashei (Lamiaceae), Palafoxia feayi (Asteraceae), and Garberia heterophylla (Asteraceae; species are hereafter referred to by their generic names). Four species were marked at the Archbold sites, and two species were marked at the Ocala sites (Table 2-1). At the Archbold burn site, 1 x 1 m random plots were established in a stratified random manner up to 10 m away from alternating sides of a 430 m transect. Random plots were established at Ocala burn and control sites in a stratified random manner along three 100 m long parallel transects at least 20 m apart at each site (Table 2-1).

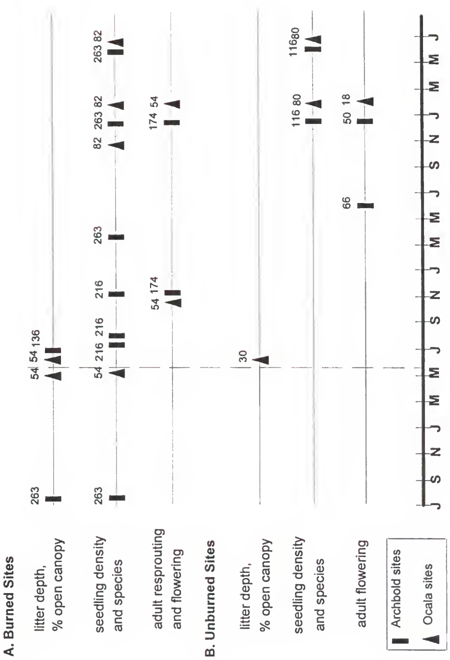
Table 2-1. Plots established on burn and control sand pine scrub sites at Archbold Biological Station and Ocala National Forest, Florida. All plots were 1 x 1 m; each nonrandom plot was centered on an adult individual of a species. Plots in burn sites were established before May 1993 prescribed burns; plots in control sites were established during the summer of 1993.

Plot types (species)	Number of plots	
	Burn site	Control site
A. Archbold Sites		
Calamintha ashei	47	--[a]
Chapmannia floridana	45	25
Eriogonum longifolium var. *gnaphifolium*	40	66
Palafoxia feayi	38	25
Random	93	--
B. Ocala Sites		
Calamintha ashei	27	25
Garberia heterophylla	27	25
Random	30[b]	30

[a] not detected near the burn site.
[b] Plots were established postfire due to prefire time constraints.

Litter depth, percent open canopy, seedling density and species, and adult plant species composition were quantified for plots in the burn sites from July 1992 to May 1993, before prescribed burns occurred (Figure 2-1). Random plots at Ocala burn and control sites, however, were an exception. Due to time constraints before the Ocala prescribed burn, random plots were established after the fire.

Figure 2-1. Time lines showing data collection for microsite variables, seedling densities and species, and adult plant resprouting and flowering in burned and unburned sand pine scrub sites at Archbold Biological Station and Ocala National Forest, Florida. Numbers above symbols represent number of 1 x 1 m plots sampled. Dashed vertical line represents the date of prescribed fires.


A. Burned Sites
litter depth, % open canopy
seedling density and species
adult resprouting and flowering
B. Unburned Sites
litter depth, % open canopy
seedling density and species
adult flowering
Archbold sites
Ocala sites
263
54
54 136
263
54 216 216
216
263
82 263 82
263 82
54 174
174 54
30
116 80
11680
66
50 18
J S N J M M J S N J M M J S N J M M J
93
94
95

Litter depth for each plot was recorded as the average of four measurements taken at random locations within the 1 m^2 area. An estimate of average percent of open canopy was made using a spherical densiometer placed in the center of each plot on the ground (Lemmon, 1957). Seedlings were defined as plants < 5 cm in height with no secondary growth aboveground, no charred stems, and with small root systems with no discernable storage tissue and no rhizome connections. Plants outside marked plots were excavated to resolve uncertainty when definition of seedlings within plots was questionable. Species of all adult plants rooted within marked plots were recorded.

Postfire Data Collection

Sites were burned using strip head fires on May 10 (Ocala) and May 25 (Archbold), 1993. Microsite characteristics, adult plant resprouting and flowering, and seedling density and species were quantified postfire during 1993 through 1995 at the two burned sites. Adult plant flowering, and seedling density and species were quantified at control sites during 1994 and 1995 (Figure 2-1). After the fires, some sample sizes were reduced due to time constraints and inability to find some plots.

Data Analysis

Patterns related to fire occurrence were quantified for microsite variables, plant species resprouting and flowering, and seedling establishment. Microsite and seedling data were analyzed separately for each site; resprouting and flowering data were analyzed across both sites. For the microsite analyses, changes in litter depth and canopy openness due to fire, plot type, or interactions between fire and plot type were characterized (Tables 2-2 and 2-3).

Table 2-2. Data analyses used to compare prefire vs. postfire microsite and seedling data from a sand pine scrub site at Archbold Biological Station, Florida. Data were collected before and after a prescribed burn conducted on May 25, 1993. Prefire data were collected during July 1992; collection dates for postfire data are in parentheses.

Response variables compared	Statistical tests
litter depths (June 1993)	repeated measures ANOVA with planned contrasts
open canopy percentages (June 1993)	repeated measures ANOVA with planned contrasts
proportion of plots with seedlings (December 1993)	McNemar change test (Siegel and Castellan 1988)
proportions of plots with seedlings among and within plot types (December 1994)	linear model categorical analysis (SAS Institute Inc. 1988)

Proportions of adults of each study species that resprouted and/or flowered within five months of burning were calculated from data collected from the Archbold and Ocala sites. Three types of analyses were conducted on the data:

1. proportions of individuals that resprouted were compared among species across both sites

2. within each species, proportions of individuals flowering were compared between the first and second years postfire
3. within each species, proportions of individuals flowering during the second year postfire were compared between burned and control sites (Table 2-4).

Table 2-3. Analyses of microsite and seedling data from sand pine scrub at Ocala National Forest, Florida burned on May 10, 1993. The first two analyses compared microsite patterns among plant-centered prefire plots on a burn site and random plots on an adjacent unburned site. The next four analyses compared prefire vs. postfire data from the burn site. Prefire data were collected May 8 - 9, 1992; collection dates for postfire data are in parentheses.

Response variables compared	Statistical tests
litter depths from prefire and unburned plots	ANOVA
open canopy percentages from prefire and unburned plots	ANOVA
litter depths (June 1993)	repeated measures ANOVA
open canopy percentages (June 1993)	repeated measures ANOVA
seedling densities (January 1995)	Wilcoxon signed ranks test (Siegel and Castellan 1988)
postfire seedling densities among plot types (January 1995)	Kruskal-Wallis test with a postiori contrasts

Seedling density medians and ranges, and proportions of plots containing seedlings, were calculated from prefire seedling counts and all postfire seedling counts at each burned site, and from seedling counts conducted in the control sites. Comparisons of prefire vs. postfire seedling occurrence were made at the site level and among plot types (i.e., species). Postfire seedling occurrence was represented by data from the December 1993 seedling count at the Archbold burned site, and data from the January 1995 count at the Ocala burned site. Data from these counts were used because they best represent the cumulative results (minus early mortality) of seedling establishment during the first year postfire.

Table 2-4. Analyses of resprouting and flowering for five perennial plant species marked in sand pine scrub sites at Archbold Biological Station and Ocala National Forest, Florida. Both sites burned in May 1993. Data collection dates are in parentheses.

Response variables compared	Statistical tests
postfire resprouting among species (Archbold: November 1993; Ocala: October 1993)	chi-square test (Siegel and Castellan 1988)
postfire flowering among species (Archbold: November 1993; Ocala: October 1993)	chi-square test
1st yr. vs. 2nd yr. postfire flowering, within species (Archbold: November 1993 and December 1994; Ocala: October 1993 and January 1995)	McNemar change test (Siegel and Castellan 1988)
flowering in burned vs. control sites, within species (Archbold: June and December 1994; Ocala: January 1995)	chi-square test

Median seedling densities from Ocala were compared to quantify differences in prefire and postfire seedling occurrence (Table 2-3). At Archbold, however, because less than half of the plots contained seedlings before and after the fire, frequencies of plots with seedlings were compared (Table 2-2).

In each site, spatial distributions of all study species seedlings with high postfire frequencies of occurrence were characterized. For each of these seedling species, a G test (Sokal and Rohlf 1981) was used to compare frequency distributions of species across all plots with an expected frequency distribution based on occurrences of seedlings of all species.

Results

Microsites

At Archbold, prefire mean litter depths for plots centered on *Calamintha*, *Eriogonum*, and *Palafoxia* were less than the mean litter depth for random plots (Dunnett's test, $p < 0.05$), but mean litter depth for *Chapmannia* plots (4.6 ± 0.4 cm) was similar to random (Figure 2-2*a*). Plots centered on adult plants at Ocala had smaller prefire litter depths than random plots (Dunnett's test, $p < 0.05$), but were not different from each other (Figure 2-2*b*). Prefire mean percent open canopy values for plots centered on all four species at Archbold were greater than the mean for random plots (Dunnett's test, $p < 0.05$; Figure 2-3*a*). Prefire mean percent open canopy values differed among all three plot types at Ocala (Dunnett's test, $p < 0.05$; Figure 2-3*b*).

The fires at both sites decreased litter depths in all plot types (fire effect $p = 0.0001$ for both sites), but

Figure 2-2. Prefire and postfire litter depths (means and standard errors) in sand pine scrub at (a) Archbold Biological Station and (b) Ocala National Forest. Sample 1 m^2 plots included random plots and plots containing adults of five herbaceous perennial and small-statured woody plant species. Sample sizes correspond to Archbold and Ocala, respectively. At Ocala, only prefire microsite data were collected for random plots.

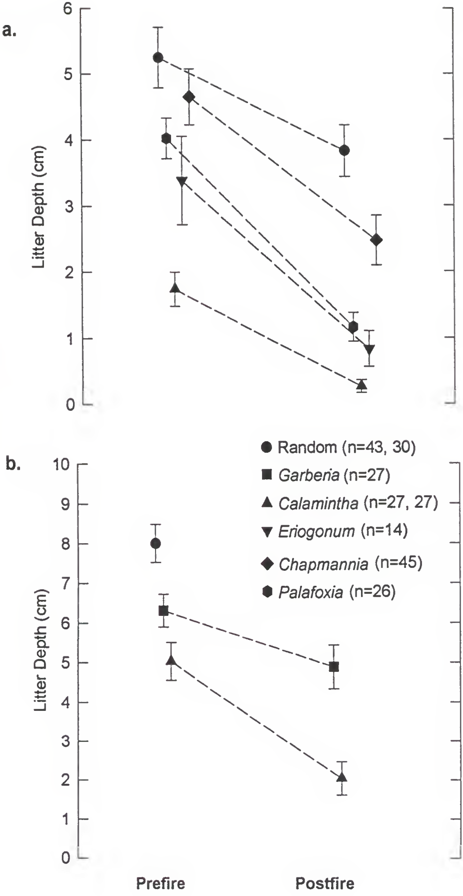
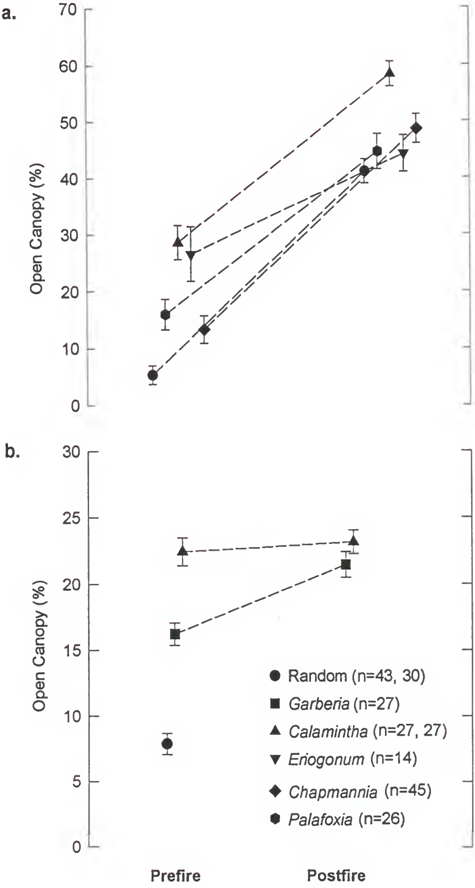

a.
Litter Depth (cm)
0
1
2
3
4
5
6
● Random (n=43, 30)
■ *Garberia* (n=27)
▲ *Calamintha* (n=27, 27)
▼ *Eriogonum* (n=14)
◆ *Chapmannia* (n=45)
⬢ *Palafoxia* (n=26)
b.
Litter Depth (cm)
0
1
2
3
4
5
6
7
8
9
10
Prefire
Postfire

Figure 2-3. Prefire and postfire percent open canopy values (means and standard errors) in sand pine scrub at (a) Archbold Biological Station and (b) Ocala National Forest. Sample 1 m^2 plots included random plots and plots containing adults of five herbaceous perennial and small-statured woody plant species. Sample sizes correspond to Archbold and Ocala, respectively. At Ocala, only prefire microsite data were collected for random plots.


a.
70
60
50
40
30
20
10
0
Open Canopy (%)
b.
30
25
20
15
10
5
0
Open Canopy (%)
● Random (n=43, 30)
■ *Garberia* (n=27)
▲ *Calamintha* (n=27, 27)
▼ *Eriogonum* (n=14)
◆ *Chapmannia* (n=45)
⬢ *Palafoxia* (n=26)
Prefire
Postfire

tended to preserve and even accentuate prefire litter depth differences among plot types (plot type effect $p < 0.001$ at both sites; plot type x fire effect $p = 0.042$ at Ocala site; Figure 2-2). The fires at both sites resulted in higher percent open canopy values in all plot types (fire effect $p < 0.05$ for both sites), and tended to reduce differences among plot types (plot type effect $p = 0.0001$ for both sites; plot type x fire effect $p < 0.01$ for both sites; Figure 2-3).

Site-level Seedling Establishment

Prefire seedling density was low at both sites (Archbold: median = 0, range = 0 - 6 seedlings/m^2; Ocala: median = 0, range = 0 - 1 seedlings/m^2), as was frequency of seedling occurrence in plots (hereafter "seedling frequency"; Figure 2-4).

At Archbold, seedling frequency increased throughout the first year after the fire to a peak of 0.50 during March 1994, then dropped by the December 1994 count. Seedling frequency in December 1994 (0.19) was higher than that before the fire (McNemar change test, $p < 0.001$), and was higher than seedling frequency in the nearby unburned site also censused in December 1994 (Figure 2-4). Median seedling density was greater than zero only in March 1994 at the burned site (median = 1; range = 0 - 22 seedlings/m^2).

Both postfire seedling frequency and postfire seedling density were higher at Ocala (October count: median = 12, range = 0 - 221 seedlings/m^2) than at Archbold. As at Archbold, seedling frequency fell by the last seedling count. Both seedling frequency and seedling density were higher in January 1995 than before the fire (Wilcoxon signed ranks test, $p < 0.0001$). Seedling frequency in January 1995 also was higher in the burned site than in the adjacent unburned site (Figure 2-4).

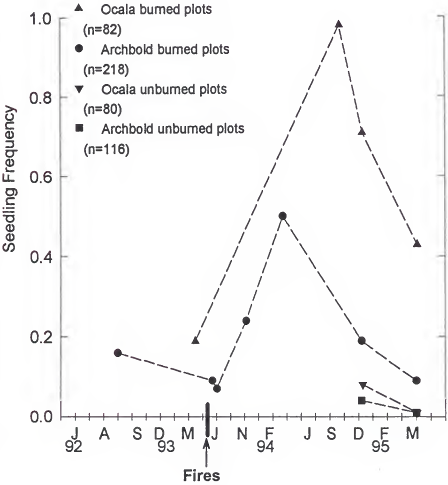


Figure 2-4. Frequency of seedlings of all species in 1 m^2 plots before and after May 1993 controlled burns in sand pine scrub at Archbold Biological Station and Ocala National Forest.

Life History Characteristics of Study Species

Resprouting and flowering

All marked Calamintha individuals at the Archbold and Ocala sites were killed by the fires. Chapmannia, Eriogonum, and Garberia, however, were strong resprouters; percentages of marked plants resprouting within five months of the fires were 100, 92, and 96, respectively. The level of resprouting for Palafoxia (64%) was lower (chi-square test, $p < 0.001$; Figure 2-5). Individuals of all resprouting species had initiated flowering by five months after the fires. Eriogonum and Garberia had higher proportions of resprouted plants flowering (95% and 100%, respectively) than Chapmannia and Palafoxia (47% and 38%, respectively; chi-square test, $p < 0.001$; Figure 2-5).

Two years postfire, the proportion of individuals flowering remained relatively low for Chapmannia and high for Garberia. In contrast, the proportion of Eriogonum individuals flowering decreased (McNemar change test, $p < 0.001$), while the proportion of Palafoxia individuals flowering increased (McNemar change test, $p < 0.001$). Flowering proportions were higher in burned sites than in unburned control sites for all species two years post-fire (chi-square test, $p < 0.05$; Figure 2-6).

Seedling establishment responses, and contributions to site-level seedling establishment

Archbold site. Of the four study species at this site, only Palafoxia seedlings were present in plant-centered and random plots before the fire. Palafoxia seedlings first appeared three weeks after the fire, and were present in low numbers in almost every postfire seedling count. Establishment of Eriogonum began five weeks postfire, and new seedlings were detected in every subsequent seedling count. Chapmannia seedlings were present only in the November 1993 (five months postfire) and March 1994 counts. Calamintha appeared late; seedlings were not detected until March 1994, ten months postfire.

Plots centered on Calamintha, Eriogonum and Palafoxia had higher seedling frequencies after the fire than did random plots (plot type effect $p = 0.0047$). Of these three species, Calamintha and Eriogonum had large postfire increases in seedling frequency (fire x plot type effect $p < 0.001$ for both species; Figure 2-7). The postfire seedling establishment responses in Calamintha and Eriogonum plots were largely due to establishment of conspecific seedlings; both species' seedlings occurred most frequently in conspecific adult plots (Table 2-5).

Ocala site. Garberia seedlings were present in low numbers before the fire. The first postfire seedling count at this site was conducted in October 1994 (16 months postfire), after seedling establishment had begun for both Calamintha and Garberia. No seedlings of either species were detected in a preliminary check in October 1993; seedling establishment for both species probably started around ten months postfire.

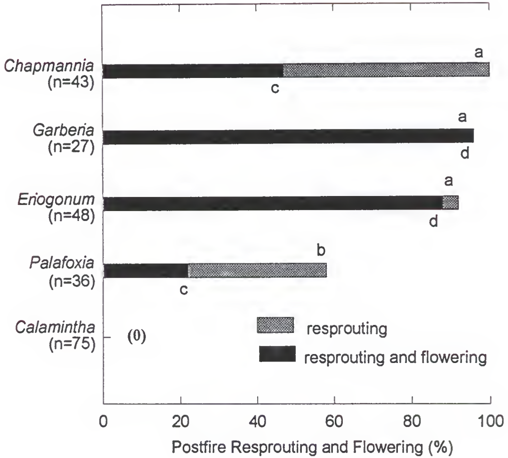


Figure 2-5. Percent resprouting and flowering of five perennial plant species five months following sand pine scrub controlled burns at Archbold Biological Station and Ocala National Forest. Plant species were Chapmannia floridana, Garberia heterophylla, Eriogonum longifolium var. gnaphifolium, Palafoxia feayi, and Calamintha ashei. Different letters above bars indicate that proportions resprouting were different among species (chi-square test, p < 0.001). Different letters below bars indicate that proportions flowering were different among species (chi-square test, p < 0.001).

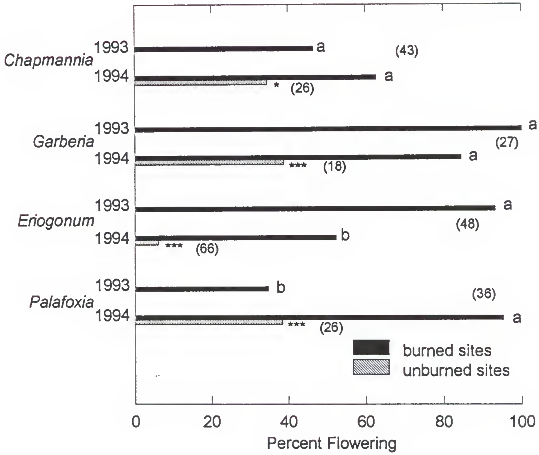


Figure 2-6. Percent flowering of four perennial plant species in paired burned/unburned sand pine scrub sites at Archbold Biological Station and Ocala National Forest. Percent flowering was quantified for resprouted individuals 5 and 19 months postfire in burned sites, and was quantified for all marked adults 19 months postfire in unburned sites. Different letters by bars indicate that flowering proportions were different between years for a species. Asterisks indicate that 1994 flowering proportion was lower in the unburned site than in the burned site for a species (*, $p < 0.05$; ***, $p < 0.001$, based on chi-square test).

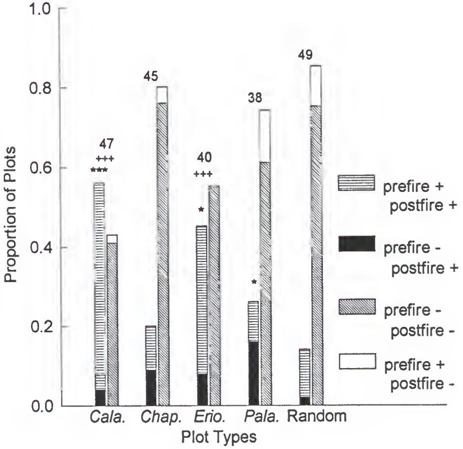


Figure 2-7. Proportions of 1 m^2 plots in four seedling prefire vs. postfire presence/absence categories (e.g., prefire +, postfire +: plots with seedlings present before and after fire; prefire -, postfire +: plots with seedlings absent before fire and present after fire) in sand pine scrub at Archbold Biological Station. Plots included random plots and plots containing adults of four herbaceous perennial and small-statured woody plant species. Seedling presence/absence data were analyzed with a linear model categorical analysis (SAS Institute Inc. 1988). Numbers above bars indicate sample sizes; symbols above bars indicate significant sources of variation in the frequency distribution:

* and ***, seedling frequency was different from random ($p < 0.05$ and $p < 0.001$, respectively);
+++, plot type x fire interaction significant ($p < 0.001$).

Table 2-5. Percent of all postfire seedlings represented by seedlings of three perennial plant species in plots of conspecific adults at two Florida sand pine scrub sites, and frequency distributions of seedlings in conspecific plots vs. plots with adults of other species. Numbers in parentheses represent expected seedling frequencies of focal species, based on seedling frequencies of all species.

Plot type	% representation of conspecific seedlings	Frequency of conspecific seedlings	Frequency of conspecific seedlings in other plot types
A. Archbold site			
Calamintha	85	22[a] (9)	3 (16)
Eriogonum	65	14[a] (4)	4 (14)
B. Ocala site			
Calamintha	48	22[a] (9)	3 (16)
Garberia	92	23 (17)	24 (30)

[a] G-test showed that seedlings occurred in plots centered on conspecific adults more often than expected ($p < 0.001$).

Postfire seedling densities in both *Calamintha* and *Garberia* plots were greater than densities in random plots (Figure 2-8). Conspecific seedlings outnumbered all other seedlings in both *Calamintha* and *Garberia* plots. Although *Calamintha* seedlings occurred most frequently in conspecific adult plots, the frequency distribution of *Garberia* seedlings did not differ from the expected distribution based on occurrences of all seedling species (Table 2-5).

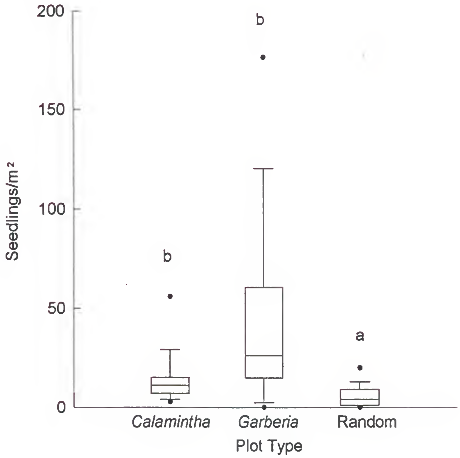


Figure 2-8. Box plots of seedling densities of all species present in nonrandom plots centered on Calamintha ashei and Garberia heterophylla, and in random plots in sand pine scrub at Ocala National Forest. Densities were quantified in January 1995, 19 months after a controlled burn. Boxes represent ranges between 25th and 75th percentiles of data. Central lines in boxes indicate 50th percentiles, capped bars indicate 10th and 90th percentiles and circles indicate 5th and 95th percentiles. Different letters indicate that seedling densities were different, based on a chi square test with a postiori contrasts ($p < 0.05$).

Discussion

Microsites

Fire effects on plot microsite characteristics at the two sites were somewhat unexpected. Although postfire litter depths declined and percent open canopy values increased as predicted, prefire patterns among plot types were largely maintained.

Before the fires, most plant-centered plots had less litter and more open canopy than random plots; i.e., the study species occurred in openings. Although canopy openings were larger after the fires, litter depth spatial patterns (but not absolute depths) remained essentially unchanged. After the fires, seedlings of most species other than study species occurred with similar frequencies in random plots and nonrandom plots (Table 2-6), suggesting that the higher postfire litter depths in random plots were not a barrier to seedling establishment. Of the three study species with increased postfire seedling establishment (i.e., Calamintha, Eriogonum and Garberia), however, seedlings of Eriogonum and Calamintha occurred almost exclusively within plots centered on conspecific adults. These patterns of seedling establishment suggest that postfire spatial recruitment patterns may be driven more by locations of adult plants than by postfire microsite patterns, especially for species with no obvious seed dispersal mechanisms.

Table 2-6. Number of postfire occurrences of seedling species in nonrandom plots centered on adults of selected small-statured perennial plant species, and in randomly located plots in sand pine scrub sites at Archbold Biological Station and at Ocala National Forest in peninsular Florida.

Species	# Occurrences in Nonrandom Plots	# Occurrences in Random Plots
A. Archbold site (nonrandom plot *n*=173; random plot *n*=93)		
Eriogonum longifolium var. *gnaphifolium* (Polygonaceae)	43	2
Calamintha ashei (Lamiaceae)	35	0
Poaceae	35	14
Dichanthelium spp. (Poaceae)	31	6
Tephrosia chrysophylla (Fabaceae)	21	10
Lupinus diffusus (Fabaceae)	15	19
Palafoxia feayi (Asteraceae)	17	9
Pinus clausa (Pinaceae)	16	15
Chapmannia floridana (Fabaceae)	16	4
Pityopsis graminifolia (Asteraceae)	5	1
Cyperus spp. (Cyperaceae)	3	4
Balduina angustifolia (Asteraceae)	3	0
Stylisma villosa (Convolvulaceae)	3	0
Chamaecrista fasciculata (Fabaceae)	1	1
Sisyrinchium solstitiale (Iridaceae)	1	0
Gratiola ramosa (Scrophulariaceae)	0	1

Table 2-6--continued.

Species	# Occurrences in Nonrandom Plots	# Occurrences in Random Plots
B. Ocala site(nonrandom plot *n*=52; random plot *n*=30)		
Garberia heterophylla (Asteraceae)	37	10
Pinus clausa (Pinaceae)	34	18
Calamintha ashei (Lamiaceae)	24	1
Rhynchospora megalocarpa (Cyperaceae)	22	8
Pityopsis graminifolia (Asteraceae)	7	2
Dichanthelium spp. (Asteraceae)	5	2
Mitchella repens (Rubiaceae)	5	0
Liatris tenuifolia (Asteraceae)	2	3
Poaceae	2	2
Cyperus spp. (Cyperaceae)	2	0
Dalea feayi (Fabaceae)	1	1
Hypericum hypericoides (Hypericaceae)	1	0
Fabaceae	1	0

Other researchers have documented the relative constancy of species composition in sand pine scrub and other fire-influenced communities during postfire vegetation regrowth (Abrahamson 1984*a*; Myers 1990, Abrahamson and Abrahamson 1996*a*, 1996*b*). In sand pine scrub, spatial patterns of openings at the ground and canopy level also may be relatively permanent despite (or perhaps because of) the occurrence of fires. Long-lasting openings may be extremely important to small nonclonal perennial species with limited seed dispersal distances, as successful completion of all life cycle stages of these species may occur primarily in openings. Periodic fires may be important in perpetuating these openings--particularly areas of sparse litter associated with openings.

Seedling Establishment and Life History Strategies

Elevated levels of seedling establishment occurred in sand pine scrub during the first year postfire. As expected with "uncoupled" recruitment, seedling densities tended to be low, particularly at Archbold. Support from this study is equivocal, however, for the prediction of small postfire seedling densities in sand pine scrub relative to other pyrogenic communities. California chaparral seedling densities, ranging from 238/m^2 five months postfire to 25/m^2 19 months postfire (Christensen and Muller 1975), were much higher than densities reported in this study, as predicted. Levels of seedling establishment following a fire in Australian heath, however, were similar to those seen at the Ocala site in this study; heath seedling densities ranged from 15/m^2 11 months postfire to 7/m^2 17 months postfire. Postfire seedling densities at two other Australian heath sites were higher, at 31/m^2 and 59/m^2 9 months and 11 months postfire, respectively (Specht et al. 1958).

Both quantitative and qualitative data support the prediction that plant species in Florida sand pine scrub have a variety of life history strategies in relation to fire (see also Menges and Kohfeldt 1995). Of the five study species, Eriogonum and Garberia are postfire flowerers; i.e., species with strong postfire seedling establishment responses following resprouting and flowering. Flowering and seedling establishment patterns for these two species were not identical, however. Eriogonum had a short, quick pulse of postfire seedling establishment, while seedling establishment for Garberia began later and lasted longer. A study quantifying plant species recovery strategies after a 1986 fire in another sand pine scrub site at Archbold (this site and the site used in the present study were probably last burned in the same fire) also showed that Garberia resprouted and established seedlings postfire, and suggested that seedling establishment continued several years after the fire (Abrahamson and Abrahamson 1996b).

Palafoxia and Chapmannia, like Eriogonum and Garberia, resprouted postfire, but did not have strong postfire seedling establishment responses; their life history strategies in relation to fire are unclear. Whereas seedling establishment for Eriogonum and Garberia seem to be closely linked to the occurrence of fire, Palafoxia and Chapmannia recruitment appears less closely linked to fire. Palafoxia individuals, however, also resprouted and established seedlings after the 1986 sand pine scrub fire at Archbold (Abrahamson and Abrahamson 1996b).

In the present study, the presence of Palafoxia seedlings before the Archbold fire and before flowering had commenced postfire suggests that seedling establishment, probably from recently-flowering adults (i.e., not from long-dormant seeds), occurs long after disturbance events. Palafoxia may have a relatively late, long-lasting peak in postfire seedling establishment, as suggested by the increase in proportion of individuals flowering during the second year postfire. Another study conducted in scrubby flatwoods sites at Archbold showed a long-lasting peak in proportion of Palafoxia plants flowering after fires; in a chronosequence of sites differing in time since last fire, proportion of plants flowering generally increased from 1 - 15 years postfire (Ostertag and Menges 1994). In addition, Palafoxia seedling establishment appeared to occur for several years after the 1986 sand pine scrub fire at Archbold (Abrahamson and Abrahamson 1996b). Chapmannia showed neither a particularly strong flowering response nor a strong seedling establishment response after fire in the present study; perhaps seedling establishment never occurs at high levels, or occurs at high levels in response to events or cues other than fires.

Calamintha was the third study species with a strong postfire seedling establishment response that appears linked to the occurrence of fire. Its seedlings probably established from seeds stored in a soil seed bank, as all of the adult individuals were killed by fire, the seeds have no obvious dispersal mechanism, and the seedlings occurred primarily within plots centered on conspecific adults.

Comparisons of plant species life forms and postfire reproductive modes from sand pine scrub in this study with similar data from California chaparral and Australian heath also support the prediction that sand pine scrub species have a variety of responses to fire. Nineteen of 37 species (51%) established seedlings postfire in sand pine scrub; 18 species resprouted, but had no postfire recruitment (Tables 2-6, 2-7 and 2-8). In contrast to sand pine scrub, much higher proportions of species established seedlings after fires in California chaparral and Australian heath; 90% and 79% of species had postfire recruitment in California chaparral and Australian heath, respectively (Vogl and Schorr 1972, Specht et al. 1958; Table 2-8).

The percentage of species with postfire seedling establishment estimated in this study (51%) is slightly lower than 57% of species reported with seedlings after fires in scrubby flatwoods (Menges and Kohfeldt 1995), a community in Florida that shares many species with sand pine scrub. For several species present in both sand pine scrub and scrubby flatwoods (e.g., Serenoa repens, Sabal etonia, Smilax auriculata, Cnidosculus stimulosus), postfire seedlings were not detected in sand pine scrub in this study (Table 2-7), but were detected in scrubby flatwoods. Most likely, seedlings were detected for more species in scrubby flatwoods than in sand pine scrub because plants in scrubby flatwoods were observed over a wider range of conditions;

plant species postfire recovery modes were recorded after fires that occurred over a period of three years.

Table 2-7. Species that resprouted and did not establish seedlings after experimental fires during May 1993 in sand pine scrub sites at Archbold Biological Station and Ocala National Forest.

Species (family)
A. Trees and shrubs
Quercus geminata (Fagaceae)
Quercus chapmanii (Fagaceae)
Quercus myrtifolia (Fagaceae)
Quercus laevis (Fagaceae)
Carya floridana (Fagaceae)
Serenoa repens (Arecaceae)
Sabal etonia (Arecaceae)
Lyonia ferruginea (Ericaceae)
Vaccinium myrsinites (Ericaceae)
Bumelia tenax (Sapotaceae)
Ilex opaca var. *arenicola* (Aquifoliaceae)
B. Perennial herbs
Licania michauxii (Chrysobalanaceae)
Smilax auriculata (Smilacaceae)
Tragia urens (Euphorbiaceae)
Stillingia sylvatica (Euphorbiaceae)
Cnidosculus stimulosus (Euphorbiaceae)
Galactia elliottii (Fabaceae)

Recruitment in sand pine scrub is relatively "uncoupled" with fire as a disturbance in comparison with California chaparral and Australian heath, based on proportions of species with postfire seedling establishment. Although a community with "uncoupled" recruitment also should have lower postfire seedling densities than those in other fire-influenced communities such as California chaparral and Australian heath, densities were not clearly lower in sand pine scrub than in other fire-influenced communities, due to wide variation in seedling densities.

Table 2-8. Number of species in life form/postfire reproductive mode categories in three pyrogenic communities.

	Florida sand pine scrub[a]	California chaparral[b]	Australian heath[c]
Seeding trees and shrubs	3	3	2
Resprouting trees and shrubs	12, 2[d]	7, 5[d]	2, 4[d]
Seeding sub-shrubs	2	18	6
Resprouting sub-shrubs	0	0	2[d]
Resprouting perennial herbs	6, 10[d]	2[d]	4, 8[d]
Geophytes	1[d]	2	1[d]
Annuals	1	24	0
Total	37	61	29

[a] from this study
[b] from Vogl and Schorr (1972)
[c] from Specht et al. (1958)
[d] species that also had postfire seedling establishment

The discrepancy in trends among communities between proportions of species with postfire seedling establishment and seedling density data is understandable in light of plant species responses to long-term vs. short-term trends in postfire conditions for seedling establishment. The proportion of species with postfire recruitment in a community is the result of selection pressure over long periods of time, with species recruitment characteristics evolving in response to long-term trends in postfire conditions for seedling establishment. The proportion of species with postfire recruitment, therefore, serves well as an index of community-level recruitment in response to the long-term influences of fire and of site-specific abiotic conditions. In contrast, postfire seedling densities should vary less in response to long-term trends in postfire conditions, and more in response to immediate conditions for seedling establishment after individual fires. Since postfire conditions that influence seedling establishment (e.g., precipitation, temperature) can vary markedly within and among pyrogenic communities, postfire seedling density at a site is not a good index of community-level response to fire over the long term.

Prefire densities of species with widely-dispersed seeds and fire histories of sites also may have influenced postfire seedling densities. Pinus clausa and Garberia, both with wind-dispersed seeds, were much more abundant at Ocala than at Archbold, and represented the highest seedling frequencies and densities at Ocala. Seeds of both of these species are dispersed postfire, and thus are generally not killed during fires.

Seeds of some of the most frequently-occurring seedling species at Archbold (e.g., Lupinus diffusus, Tephrosia chrysophylla) were present in the soil before the fire. Mortality of buried seeds during the long time period without fire, and/or mortality during the fire may have diminished potential postfire establishment levels. In other studies conducted at Archbold, plant recruitment also appeared sparse after fires in long-unburned sand pine scrub, flatwoods and scrubby flatwoods sites (Abrahamson and Abrahamson 1996a, 1996b).

Different long-term fire histories at the study sites may be responsible for differences in species composition (and thus potential postfire seedling recruitment). Although time since last fire was similar in the two sites, historic fire frequencies almost certainly were different. At Ocala, infrequent fires before the 1935 fire probably enabled sand pine and other postfire recruiting species to persist and reach high densities, while frequent fires before 1927 at Archbold may have favored postfire resprouters such as oaks and grasses over postfire recruiters.

This research suggests that postfire recruitment in Florida sand pine scrub is influenced by prefire spatial patterns of microsite openings and adult plants. Results showed that although recruitment of some species is closely linked to fire occurrence, recruitment at the community level in Florida sand pine scrub is "uncoupled" (sensu Grubb) to fire compared to recruitment in California chaparral and Australian heath. Research on sand pine scrub sites encompassing a range of postfire-recruiting species densities and historic fire frequencies is needed to test the generality of these results.

CHAPTER 3

SOIL TEMPERATURES AND SEED SURVIVAL IN FLORIDA SAND PINE SCRUB

Introduction

Seeds that survive fires in the soil contribute to postfire recruitment to varying degrees among fire-influenced communities (e.g., Lyon and Stickney 1976, Parker and Kelly 1989). The capacity of species in these communities to establish seedlings after fire from seeds in a soil seed bank should be influenced by several factors, including (1) magnitude and duration of high or elevated temperatures during fire at soil depths and in microsites where viable seeds are located, and (2) seed germination responses to elevated temperatures.

A large volume of field research and laboratory research has been conducted on temperatures reached during natural fires (e.g., Heyward 1938, Beadle 1940, Whittaker 1961, Floyd 1966, Kayll 1966, Scotter 1970, Shea et al. 1979, Gill and Groves 1981, Hobbs et al. 1984, Patten and Cave 1984, Auld 1986, Stott 1986, Hobbs and Atkins 1988, Muñoz and Fuentes 1989, Bradstock et al. 1992, Miranda et al. 1993, Bradstock and Auld 1995), and on seed germination responses to elevated temperatures (e.g., Beadle 1940, Went et al. 1952, Stone and Juhren 1953, Hadley 1961, Floyd 1966, Martin et al. 1975, Shea et al. 1979, Keeley et al. 1985, Auld 1986, Keeley 1987, Barro and Poth 1988, Muñoz and Fuentes 1989, Auld and O'Connell 1991, Keeley 1991, Roy and Sonié 1992, González-Rabanal et al. 1994). These two lines of research have usually been mutually exclusive, and have concentrated largely on Mediterranean-climate ecosystems and their species.

Researchers generally have used either temperature-sensitive paints or thermocouples to quantify soil temperatures reached during fires. Although recorded temperatures have varied among ecosystems and with differences in burning conditions, several patterns have been consistent across studies. Maximum soil temperatures generally decrease as depth in the soil increases, but durations of high temperatures increase (Heyward 1938, Floyd 1966, Shea et al. 1979, Patten and Cave 1984, Auld 1986, Muñoz and Fuentes 1989, Bradstock et al. 1992, Miranda et al. 1993, Bradstock and Auld 1995). Soil temperatures reached during fires also tend to vary with microsites, with temperatures in open microsites lower than temperatures in microsites with higher fuel accumulations (Patten and Cave 1984, Hobbs and Atkins 1988).

In laboratory germination studies, plant species from several ecosystems have demonstrated positive germination responses after being exposed to temperatures typically reached during fires. Taxa or functional groups with this response include legumes in the southeastern United States, California and Australia (Went et al. 1952, Martin et al. 1975, Shea et al. 1979, Keeley et al. 1985, Auld 1986, Auld and O'Connell 1991), obligately-seeding shrubs in California chaparral and in southern France (Went et al. 1952, Hadley 1961, Keeley 1987, Roy and Sonié 1992), and annual species in California chaparral (Went et al. 1952, Keeley et al. 1985). Other species, however, have responded to elevated temperatures with decreased or no germination. Some functional groups that have demonstrated this response are herbaceous perennials (Keeley et al. 1985) and other species that do not establish seedlings after fires (Keeley 1987).

This study documents soil temperatures during fires, and seed germination responses to elevated temperatures in sand pine scrub, a community occurring primarily in Florida on well-drained sandy soils of former Miocene to Pleistocene dunes. Sand pine scrub is dominated by woody shrubs including several oak species (Quercus spp.), rusty lyonia (Lyonia ferruginea), Florida rosemary (Ceratiola ericoides), and occasionally scrub hickory (Carya floridana); often an overstory of sand pine (Pinus clausa) is present (Myers 1990). Small-statured (< 2 m tall) perennial species are usually sparse, and annual species are virtually absent.

Natural fires are lightning-initiated, and usually occur during the wet growing season. Although frequency of lightning strikes is extremely high in Florida (Lopez and Holle 1987), sand pine scrub fires occur infrequently, approximately every 10 to 100 years. A combination of fuel characteristics and season of burning influences fire frequency--ground litter and other fine fuels are often sparse, most living vegetation is neither highly flammable nor easily ignited, and fuels are rarely dry during the lightning season. Consequently, fires tend to occur under extreme conditions of high fuel buildup, dry weather, or high winds, and often are intense (Myers 1990).

As in other fire-influenced communities, plant species in sand pine scrub vary in their responses to fire. Most woody shrub species resprout and do not establish seedlings immediately following fires. In contrast, seedling establishment occurs primarily or exclusively after fire for some plant species that are killed by fire (e.g., *Pinus clausa*, *Ceratiola ericoides*, *Dicerandra frutescens*, *Calamintha ashei*; Johnson and Abrahamson 1990, Myers 1990, Menges 1992, Menges and Kohfeldt 1995), as well as for some small-statured species that resprout following fire (e.g., *Eriogonum longifolium* var. *gnaphifolium*, *Garberia heterophylla*; Abrahamson and Abrahamson 1996*b*, Chapter 2).

Although heat- and smoke-induced germination have not been documented in sand pine scrub as in some other fire-influenced communities (e.g., Keeley 1991, Le Maitre and Midgley 1992), seeds of some sand pine scrub species germinate after surviving fire in a soil seed bank (Johnson 1982, Menges 1992). In a recent study conducted at Archbold Biological Station, viable seeds were present in soil samples collected less than three months after fires, from 0 - 7 cm depth in the soil (Kohfeldt personal communications).

Temperatures reached during fires and germination responses to those temperatures are virtually unknown for sand pine scrub; soil temperatures during fire apparently have never been measured, and germination responses to high temperatures of most species have not been studied. Information on soil temperatures during fires and germination responses after fires should further elucidate the plant community response to fire in sand pine scrub, and could potentially increase effectiveness of rare species conservation through use of fire.

The first of two objectives of this study was to measure soil temperatures at different depths and in different microsites during fires in sand pine scrub. Lower peak soil temperatures and longer temperature durations were expected with increasing depth in the soil, as documented in other studies. Spatial patterns of combustible fuel in sand pine scrub are defined primarily by a widespread matrix of woody shrub vegetation underlain by moderate amounts of ground litter, interspersed with canopy openings with little or no litter. In this study, soil temperatures in microsites under vegetation (e.g., shrubs) were expected to be higher than those in openings.

The second objective of this study was to quantify germination responses of two small-statured perennial species after exposing the seeds to temperatures typically reached during sand pine scrub fires. Small-statured perennial species were chosen for study because much of the postfire seedling establishment response in sand pine scrub is attributable to species from this general group (Chapter 2). The two study species (hereafter referred to by their generic names), Eriogonum longifolium var. gnaphifolium (Polygonaceae; Reveal 1981) and Garberia heterophylla (Asteraceae), were chosen because (1) both species establish seedlings primarily after fire; (2) although both species are relatively common locally, they are endemic to Florida, occur primarily in sand pine scrub, and are subjects of conservation concern (Eriogonum longifolium var. gnaphifolium is federally listed as threatened).

Eriogonum is an herbaceous perennial and Garberia is a woody shrub; both species have strong postfire resprouting and flowering responses (Chapter 2). As documented for other herbaceous perennials, germination was expected to decrease for Eriogonum seeds after exposure to an elevated temperature. Seeds of resprouting shrub species have exhibited a variety of responses to high temperatures, making the Garberia germination response in this study potentially less predictable. Garberia seeds, however, readily imbibe water and lack the hard seed coat common to many species with heat-stimulated germination (personal observations). Consequently, in this study Garberia seed germination was expected to decrease after exposure to an elevated temperature.

Methods

Field Experiments

Study areas were sand pine scrub sites at Ocala National Forest in Marion County, Florida (29° 08', 81° 45') and Archbold Biological Station in Highlands County, Florida (27° 15', 81° 15'). The Ocala site and Archbold site last burned in 1935 and 1927, respectively. Both sites had a dense shrub layer consisting primarily of several species of oaks (*Quercus* spp.). Overstories differed in the two sites, however; sand pine was the only species in the overstory at Ocala, while at Archbold sand pines were interspersed with south Florida slash pines (*Pinus elliottii* var. *densa*).

Controlled burns were conducted at the Ocala and Archbold sites on May 10, 1993 and May 25, 1993, respectively. Before each fire, a datalogger (21X Micrologger, Campbell Scientific, Inc.) connected to 16 copper-constantan, 0.51 mm diameter thermocouples via insulated leads was buried in the site to be burned. The thermocouple leads were 1.5 - 4 m long, and were buried approximately 2 cm deep; the datalogger was placed in a fiberglass case and buried approximately 50 cm deep.

Each thermocouple was placed either at the soil surface or at 2 cm depth, and either in an open microsite or under vegetation; each depth - microsite combination was replicated four times. Adjacent to each thermocouple, a glass petri dish containing 10 *Eriogonum* seeds was placed at the same soil depth and microsite. In each petri dish, Eriogonum seeds were placed on top of a layer of sand completely covering the bottom of the petri dish. Six petri dishes with Eriogonum seeds also were placed at a nearby control site that did not burn.

At Archbold the sides of each petri dish were painted with 19 temperature-sensitive paints (Tempilaq, Tempil Division, Big Three Industries, Inc.). Manufacturer-specified melting temperatures of paints ranged from 37.8 °C to 815.6 °C. In addition to petri dishes adjacent to thermocouples, petri dishes also were placed throughout the site so that each depth - microsite combination was replicated eight additional times.

During each fire, the datalogger recorded thermocouple temperatures every five seconds. Temperature recording occurred from 90 minutes before the fire until 90 minutes after the flame front went through at the Ocala site, and from 90 minutes before the fire to 60 minutes after the flame front went through at Archbold.

After each fire, the datalogger and all petri dishes were recovered. Intact seeds were extracted from soil in the petri dishes, and were classified as charred or uncharred. All uncharred seeds were placed on moist filter paper in clean petri dishes, and observed for germination for one month. Viability of ungerminated seeds was assayed with a tetrazolium test (Lakon 1949). At Archbold, maximum temperature reached during the fire was quantified for each petri dish by determining which temperature-sensitive paints melted.

Data on thermocouple maximum temperatures and temperature durations were analyzed separately for the Archbold and Ocala fires. Analyses of variance were conducted on rank-transformed maximum thermocouple temperatures to detect differences due to depth in the soil and microsite (SAS Institute Inc. 1988). Temperature duration was defined for each thermocouple as the length of time that 75% of the maximum thermocouple temperature was maintained or exceeded. Kolmogorov-Smirnov tests were used to compare median temperature durations between thermocouples placed at the soil surface and those placed at 2 cm depth (Siegel and Castellan 1988).

Maximum temperatures during the Archbold fire of petri dishes placed at the soil surface and at 2 cm depth were compared using a chi-square test, and a t-test was used to compare maximum temperatures of petri dishes and adjacent thermocouples. Data from both fires on Eriogonum seeds recovered from petri dishes were combined to determine the immediate fire effect on the seeds. Numbers of petri dishes with charred Eriogonum seeds at the soil surface and at 2 cm depth were compared using a chi-square test.

Laboratory Experiments

Seeds of Eriogonum and Garberia were observed for germination after being exposed to a control temperature (25

°C) and elevated temperatures and durations representative of those sustained at the soil surface and at 2 cm depth during the experimental fires. Elevated temperatures used were 100 °C (commonly sustained at the soil surface for 4 - 6 min, but usually not reached at 2 cm depth) and 60 °C (commonly sustained at 2 cm depth for 4 to > 91 min).

Experiments were conducted from December 8 - 17, 1993, and from December 14, 1995 to January 7, 1996 for Eriogonum and Garberia seeds, respectively. Separate experiments, using 160 seeds in each, were conducted for each species and for each elevated temperature. Half of the seeds were placed in a drying oven and exposed to the elevated temperature for five minutes or 30 minutes in the experiments using 100 °C and 60 °C, respectively. The remaining seeds in each experiment were kept at room temperature. Then seeds were placed on moist filter paper in petri dishes and observed for germination. Seed germination responses were compared between 25 °C and 100 °C treatments using Fisher exact tests (Siegel and Castellan 1988); t-tests were used to compare germination responses between 25 °C and 60 °C treatments.

To determine times required to melt temperature-sensitive paints on petri dishes, trials were conducted in which a petri dish painted with a temperature-sensitive paint was placed in a muffle furnace (Thermolyne, Sybron Corporation) with the door open, and timed until the paint melted. Five to 14 trials were conducted for each of 13 paints, with manufacturer-specified melting temperatures ranging from 37.8 °C to 704.4 °C.

Results

Field Experiments

Weather conditions and fire characteristics were similar for the two fires, but flame lengths in the Archbold fire were greater than those in the Ocala fire (Table 3-1).

Table 3-1. Weather conditions and fire characteristics for Florida sand pine scrub fires at Ocala National Forest and Archbold Biological Station during May 1993.

	Ocala	Archbold
Date of fire	May 10, 1993	May 25, 1993
Time of measurements	1150 - 1205	1259 - 1305
Air temperature	28 °C	29 °C
Relative humidity	46%	52%
Wind speed	0.89 m/s	0.54 m/s
Wind direction	SE	SE
Flame lengths	3 - 5 m	6 - 15 m
Rate of fire spread	12 m/min	12 m/min

Temperatures quantified with thermocouples

Although soil temperatures and their temporal patterns varied widely both within and between microsite treatment combinations during both fires (Figures 3-1 and 3-2), temperatures were higher at the soil surface than at 2 cm depth as expected (Table 3-2). Temperatures at the soil surface reached maxima of 621.7 °C and 628.8 °C during the Archbold and Ocala fires, respectively; however, maximum temperatures at 2 cm depth were less than half those at the surface (Figures 3-1 and 3-2). The higher temperatures at the soil surface also had shorter durations than temperatures at 2 cm depth (Table 3-3).

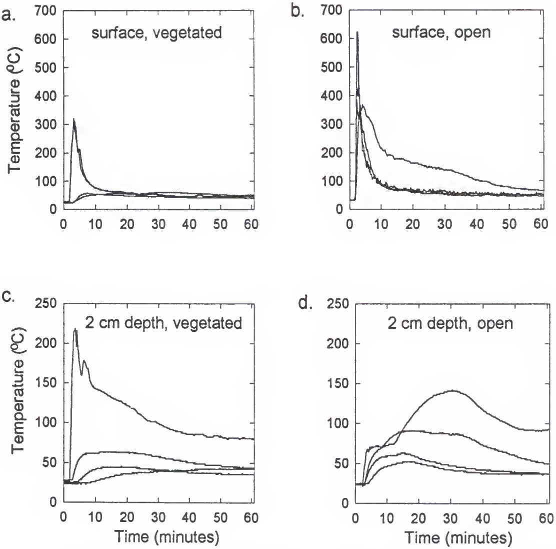


Figure 3-1. Soil temperatures during a prescribed sand pine scrub fire at Archbold Biological Station, Florida on May 25, 1993. Temperatures were recorded with copper-constantan thermocouples placed at the soil surface in vegetated (a) and open (b) microsites, and at 2 cm depth in vegetated (c) and open (d) microsites. Each depth - microsite combination was replicated four times. Note different scales of y-axes.

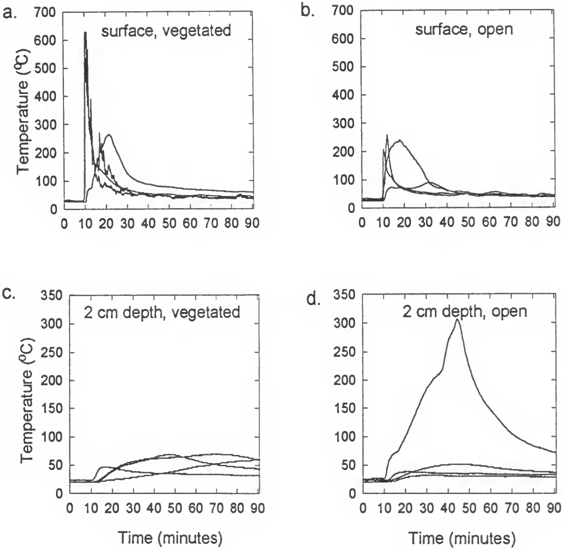


Figure 3-2. Soil temperatures during a prescribed sand pine scrub fire at Ocala National Forest, Florida on May 10, 1993. Temperatures were recorded with copper-constantan thermocouples placed at the soil surface in vegetated (a) and open (b) microsites, and at 2 cm depth in vegetated (c) and open (d) microsites. Each depth - microsite combination was replicated four times. Note different scales of y-axes.

Table 3-2. Effects of soil depth and microsite on maximum temperatures recorded during controlled burns in sand pine scrub at Archbold Biological Station and Ocala National Forest, Florida. Temperatures were recorded with copper-constantan thermocouples placed at the soil surface or at 2 cm depth, and in open or vegetated microsites. Data were rank-transformed prior to the ANOVA.

Source	SS	df	F ratio	P
A. Archbold fire				
Depth	121.0	1	11.2	$0.005 < p < 0.01$
Microsite	64.0	1	5.9	$0.025 < p < 0.05$
Depth x microsite	25.0	1	2.3	$p > 0.10$
Error	130.0	12		
B. Ocala fire				
Depth	182.3	1	19.5	$p < 0.005$
Microsite	25.0	1	2.7	$p > 0.10$
Depth x microsite	20.3	1	2.2	$p > 0.10$
Error	112.5	12		

Temperatures in vegetated vs. open microsites differed from predicted patterns, however. Temperatures during the Archbold fire were higher in open microsites than in vegetated microsites (Table 3-2), in contrast to the expected trend. Although temperatures during the Ocala fire tended to be higher in vegetated than in open microsites, a large range of temperatures within microsites resulted in no statistically significant difference in temperatures between microsites (Table 3-2).

Temperatures quantified with temperature-sensitive paints

As with thermocouple-quantified temperatures, patterns of melted paints on petri dishes at Archbold showed that maximum soil temperatures were higher at the surface than at 2 cm depth ($\chi_1^2 = 33.6$, $p < 0.001$). Maximum temperatures of petri dishes placed at the soil surface varied widely. Most temperatures ranged from 93 °C to 315 °C, but 4 of 24 surface petri dishes reached temperatures > 343 °C, while 2 surface/open petri dish temperatures were < 37.8 °C (Figure 3-3). In contrast, maximum temperatures of petri dishes placed at 2 cm depth were more similar; only 1 of 24 petri dishes placed at 2 cm depth exceeded 100 °C (Figure 3-3). Although differences between temperatures of petri dishes in open vs. vegetated microsites were not tested statistically due to small sample sizes, temperatures appeared similar among microsites (Figure 3-3).

Table 3-3. Temperature durations of copper-constantan thermocouples placed at the soil surface or at 2 cm depth in the soil. Temperatures were quantified during prescribed fires conducted during May 1993 at Archbold Biological Station and Ocala National Forest, Florida. Temperature duration was defined as the length of time that 75% of the maximum thermocouple temperature was maintained or exceeded. Kolmogorov-Smirnov tests were used to detect differences in temperature durations with depth in soil.

	Depth in Soil (n = 4)	Temperature Duration (s) (median (range))
A. Archbold fire		
	0 cm	105 (20 - >3260)
	2 cm	2020 (160 - >3250)[a]
B. Ocala fire		
	0 cm	80 (65 - 1555)
	2 cm	2918 (675 - >4625)[b]

[a] $p = 0.05$
[b] $p < 0.01$

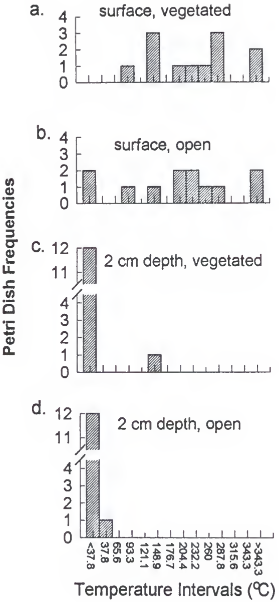


Figure 3-3. Frequency distributions of maximum petri dish temperatures during a prescribed sand pine scrub fire at Archbold Biological Station, Florida on May 25, 1993. Temperatures were quantified with temperature-sensitive paints on the petri dishes; temperature intervals for the frequency distributions represent melting points of the paints. Petri dishes were placed at the soil surface in vegetated (a) and open (b) microsites, and at 2 cm depth in vegetated (c) and open (d) microsites; each depth - microsite combination was replicated 12 times.

Comparison of thermocouple maximum temperatures with maximum temperatures of adjacent petri dishes showed that temperatures quantified via the two methods differed (t = 25.0, $0.02 < \underline{p} < 0.05$; Table 3-4). Part of this discrepancy in temperatures may be due to underestimation of maximum temperatures by temperature-sensitive paints on glass petri dishes; time periods required for petri dish heating and paint melting (Figure 3-4) may impede detection of short-duration temperature peaks.

Table 3-4. Maximum temperatures at 0 cm or 2 cm depth in soil, and in open or vegetated microsites, during a prescribed fire in sand pine scrub at Archbold Biological Station, Florida. Temperatures were quantified with copper-constantan thermocouples and with temperature-sensitive paints placed on adjacent glass petri dishes.

Depth	Microsite	Maximum Temperature (°C) Thermocouple	 Paint[a]
0 cm	open	621.7	163.7
0 cm	open	436.2	107.2
0 cm	open	383.5	287.8
0 cm	open	367.8	< 37.8
0 cm	vegetated	308.1	260.0
0 cm	vegetated	59.8	287.8
0 cm	vegetated	319.8	232.2
0 cm	vegetated	56.9	162.8
2 cm	open	63.0	37.8
2 cm	open	90.4	< 37.8
2 cm	open	52.0	< 37.8
2 cm	open	141.7	< 37.8
2 cm	vegetated	218.3	< 37.8
2 cm	vegetated	63.0	< 37.8
2 cm	vegetated	45.6	< 37.8
2 cm	vegetated	43.6	< 37.8

[a] Temperatures represent the manufacturer-specified melting temperatures of the paints that melted.

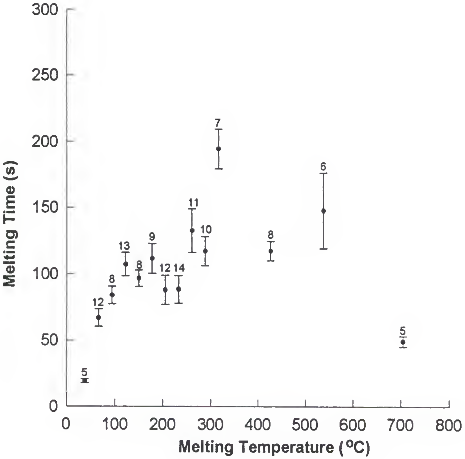


Figure 3-4. Melting times (mean ± S.E.) of temperature-sensitive paints (Tempilaq, Tempil Division, Big Three Industries, Inc.) on glass petri dishes. The number above each symbol represents the number of melting trials conducted for that paint. In each trial a petri dish was placed in a muffle furnace set at the manufacturer-specified melting temperature of the paint on the dish, and melting time was quantified.

Survival of seeds in petri dishes

Most uncharred *Eriogonum* seeds recovered after both fires were from petri dishes placed at 2 cm depth (Table 3-5). Of 34 petri dishes recovered from the soil surface after the fires, only one dish contained uncharred seeds. Numbers of petri dishes with charred seeds did not appear to differ between open and vegetated microsites, although differences were not tested statistically due to small sample sizes (Table 3-5).

Table 3-5. Number of petri dishes from which charred *Eriogonum longifolium* var. *gnaphifolium* seeds were recovered after controlled burns in sand pine scrub at Archbold Biological Station and at Ocala National Forest, Florida, vs. number of petri dishes from which all seeds were recovered uncharred; and total number of uncharred seeds recovered. Petri dishes were placed at 0 cm or 2 cm depth in the soil, and in open or vegetated (from 0 - 2 m vegetation height) microsites. Each petri dish contained ten seeds.

Microsite Type	# petri dishes with charred seeds	# petri dishes without charred seeds[a]	Total # uncharred seeds
0 cm/open	17	0	0
0 cm/vegetated	16	1	10
2 cm/open	3	14	154
2 cm/vegetated	3	14	156

[a] More petri dishes with uncharred seeds were recovered from 2 cm depth ($\chi_1^2 = 44.0$, $p < 0.001$).

No seeds germinated during trials using uncharred seeds recovered after the fires. Tetrazolium tests on seeds that were collected at the same time as seeds used in the experimental fires indicated that viability was 34 ± 4% (mean ± S.E.).

Laboratory Experiments

In both Eriogonum and Garberia experiments 100 °C was lethal to seeds; no seeds exposed to 100 °C for five minutes germinated, while seeds exposed to room temperature germinated in all petri dishes (Table 3-6). Seeds of both species also behaved similarly when exposed to 60 °C for 30 minutes; seeds germinated from all petri dishes in both experiments, with no differences in numbers germinating between seeds exposed to 60 °C and seeds exposed to room temperature (Eriogonum: $t = 1.27$, $p = 0.25$; Garberia: $t = 0.397$, $0.5 < p < 0.9$; Table 3-7).

Table 3-6. Number of petri dishes from which Eriogonum longifolium var. gnaphifolium (Polygonaceae) and Garberia heterophylla (Asteraceae) seeds germinated after being exposed to 100 °C or 25 °C for 5 minutes. Germination trials were conducted from December 8 - 17, 1993, and from December 14, 1995 to January 2, 1996 for Eriogonum and Garberia, respectively.

	Temperature (°C)	Number of Petri Dishes[a] (n = 4)
A. *Eriogonum* seeds		
	25	4
	100	0[b]
B. *Garberia* seeds		
	25	4
	100	0[b]

[a] Each petri dish contained 20 seeds.

[b] Fisher exact test showed a reduction in germination with $p = 0.0143$.

Table 3-7. Numbers (mean ± S.E.) of Eriogonum longifolium var. gnaphifolium (Polygonaceae) and Garberia heterophylla (Asteraceae) seeds that germinated after being exposed to 60 °C or 25 °C for 30 minutes. Germination trials were conducted from December 8 - 17, 1993, and from December 30, 1995 to January 7, 1996 for Eriogonum and Garberia, respectively. Identical superscripts within a row indicate no difference in germination between temperature treatments (t-test, p > 0.05).

	# germinated seeds (mean ± S.E.)	
	Temperature treatments[†]	
Species	25 °C	60 °C
Eriogonum longifolium var. gnaphifolium	15.0 ± 1.6^{a}	11.5 ± 2.3^{a}
Garberia heterophylla	19.0 ± 0.4^{a}	19.3 ± 0.5^{a}

[†] n = 4 petri dishes, each with 20 seeds

Discussion

Soil Temperatures during Fires

Depth in the soil has a strong influence on magnitude and variability of temperatures during Florida sand pine scrub fires, and thus influences seed survival during fires. As expected, maximum temperatures at the soil surface were higher and peak temperature durations were shorter than at 2 cm depth. Less predictable, however, were (1) effects of microsites at the soil surface on maximum temperatures; and (2) detailed spatial patterns of temperatures at the soil surface, and their implications for seed survival.

The effect of microsites on soil temperatures was different from that predicted, and was different between the two fires. Differences in overstory pine species and resulting litter characteristics between the sites contributed to the different microsite effects. Sand pine, the only tree species at Ocala, produces sparse litter consisting of short needles, but south Florida slash pine has much longer and more flammable needles than sand pine, and produces more litter. Since south Florida slash pine was present only at Archbold, different types and amounts of pine litter had accumulated in open microsites in the two sites; litter in vegetated microsites consisted primarily of sclerophyllous leaves with comparatively low flammability.

During the Ocala fire, a high variance in temperatures within microsites precluded detection of a microsite effect. During the Archbold fire a microsite effect was detected, but the pattern of temperatures between open and vegetated microsites was the reverse of the expected pattern. Higher maximum temperatures in open microsites were probably due to the well-aerated, relatively flammable slash pine litter in open microsites burning more completely and at higher temperatures than the more compacted, less flammable oak and hickory litter in vegetated microsites (Abrahamson 1984a). As reported in other studies (Patten and Cave 1984, Stott 1986, Hobbs and Atkins 1988), patterns of soil temperatures during fires appear to be related more directly to litter (i.e., fuel) type and amount than to microsites defined in this study.

Not only was the effect of microsites on soil temperature unpredictable, but temperatures at the soil surface in general were unpredictable when compared to temperatures at 2 cm depth. Soil surface temperatures, in addition to having greater variation among experimental locations than at 2 cm depth, varied widely both in time and in space within experimental locations, as demonstrated by temperatures recorded with thermocouples and with temperature-sensitive paints. Temperatures recorded by thermocouples at the soil surface generally increased to extremely high, brief maxima, thereby producing many within-location combinations of temperatures and temperature durations. As a consequence of this high variation in temperatures over time, temperature-sensitive paints on petri dishes usually underestimated maximum temperatures of adjacent thermocouples at the soil surface. The maximum temperatures recorded by temperature-sensitive paints apparently were the highest temperatures that persisted long enough to melt the corresponding paints. As might be predicted by the variation in patterns of thermocouple temperatures vs. time, differences between maximum temperatures of petri dishes and adjacent thermocouples varied widely.

Differences between petri dish and adjacent thermocouple temperatures at Archbold also indicated that soil temperatures varied spatially within experimental locations. Because maximum temperatures recorded by temperature-sensitive paints often differed from those expected based on temperature patterns of adjacent thermocouples (Table 3-4, Figure 3-1), temperatures and temperature durations must have varied over a very small spatial scale.

Seed Survival during Fires

Since virtually all maximum temperatures at the soil surface were ≥ 100 °C and lethal to Eriogonum and Garberia seeds, much of the variation in soil surface temperatures during fires was irrelevant to seed survival for these species. Such extremely variable but high temperatures also should be lethal to most other species of seeds; in other studies, even seeds for which germination increased after exposure to high temperatures were usually killed by temperatures ≥ 120 - 150 °C (Auld and O'Connell 1991). Nevertheless, a fraction of seeds at the soil surface may survive fires in sand pine scrub, since Eriogonum seeds in one petri dish at the soil surface remained uncharred, and soil surface temperatures presumably were heterogeneous at a very small scale.

Seed survival is more likely and more predictable at 2 cm depth in the soil, since soil temperatures during fires were relatively low, and varied little from site to site. Although higher proportions of seeds should survive through fire at this depth in the soil, some seed mortality must occur, since lethal temperatures were occasionally reached.

For species that rely on recruitment from seeds that survive through fire, a tradeoff exists between higher probability of survival and increasing difficulty of seedling emergence with increasing depth in the soil. Seedlings from larger seeds should emerge from 2 cm depth with little difficulty, as has been demonstrated for several legume species with seed masses near 30 mg (Shea 1979, Auld 1986, Auld and O'Connell 1991). Eriogonum and Garberia seeds, however, are much smaller; seeds of both species have an average mass of 3.7 ± 0.1 mg. Their seeds may be incapable of germination and seedling emergence from 2 cm depth, especially since litter apparently acted as a mechanical barrier to Eriogonum seedling emergence in another experiment (Chapter 4).

The extremely limited capacities for Eriogonum and Garberia seed survival through fires are consistent with postfire recruitment characteristics for these species. In a concurrent study of seedling recruitment following the experimental fires, Eriogonum and Garberia seedlings germinated from seeds produced after the fires by resprouting adults. Seeds of some species quantified as seedlings after the fires (e.g., Calamintha ashei, Lupinus diffusus, Tephrosia chrysophylla), however, presumably germinated after surviving through the fires, as adults of the species were killed by the fires and seeds had no obvious long-distance dispersal mechanisms (Chapter 2). Although seed germination characteristics for these adult-killed species are unknown, seeds probably were capable of germinating after exposure to elevated temperatures (i.e., ~

60 - 100 °C). Seeds germinated either at the soil surface in microsites that failed to reach lethal temperatures, or at depths beneath the soil surface from which seedlings could emerge.

This study not only showed that patterns of temperatures differ between the soil surface and 2 cm depth, but also demonstrated differences in relative strengths and weaknesses of two temperature quantification methods. Temperature-sensitive paints on petri dishes were much less precise than thermocouples in quantifying maximum temperatures; therefore, results from temperature-sensitive paints were reliable only at 2 cm depth, where temperature durations were long. Nevertheless, temperature-sensitive paints are adequate for documenting large differences in temperatures between depths in the soil, and for recording maximum temperatures beneath the soil surface, where relatively large proportions of seeds should survive through fires.

In addition to maximum temperatures, temperature durations influence seed survival through fires. Since (1) variation in temperature durations and spatial variation in maximum temperatures at the soil surface are potentially relevant to seed survival, and (2) thermocouples can quantify temperature durations and complex spatial patterns in temperatures, thermocouples should be used in studies of temperatures relevant to seed survival during fires to quantify temperature patterns at the soil surface.

Results from this study suggested that small-scale spatial variation in temperature exists at the soil surface during fires, and that low-temperature patches are essential for seed survival on the soil surface. Additional studies are needed to document small-scale patterns of temperatures, temperature durations, and seed survival at the soil surface during fires. Seed survival through fire and germination after fire, however, are only a small part of the process of postfire recruitment. Future research on topics such as effects of postfire microsite conditions on seedling establishment, and the relevance of postfire microsite conditions to the evolution of seed germination characteristics, will contribute to a comprehensive characterization of postfire recruitment.

CHAPTER 4

EFFECTS OF SHADING, LITTER AND WATERING ON SEEDLING ESTABLISHMENT OF TWO POSTFIRE-RECRUITING SPECIES IN FLORIDA SAND PINE SCRUB

Introduction

Natural disturbances are thought to maintain plant species diversity through increasing the availability of resources needed for establishment and survival of some species (e.g., Platt 1975, Tilman 1982, Christensen 1985, Denslow 1985). In the case of natural fires, increased plant species recruitment has been shown to closely follow fire occurrence in several communities (Specht et al. 1958, Christensen and Muller 1975, Keeley et al. 1981, Whelan 1985).

Although growth and survival of established plants may be enhanced following fires due to reduced competition and increased availability of resources such as light, water, and some nutrients (Christensen and Muller 1975, Wellington and Noble 1985), conditions may be relatively harsh for seed germination and early seedling establishment during the first postfire growing season (Christensen and Muller 1975, Christensen 1985, Frazer and Davis 1988). Through consuming litter and reducing canopy cover, fires may create unsheltered microsites that are too dry and/or hot for successful seed germination and seedling establishment. Recruitment of some species, therefore, may occur in remaining sheltered microsites, may occur only after substantial rainfall, or may be delayed until litter accumulation and canopy regrowth modify soil surface conditions.

Conditions for plant species recruitment from seed may be especially harsh following fires in Florida inland peninsular sand pine scrub. This shrub-dominated community occurs on well-drained, sandy soils, and burns every 10 to 100 years in intense fires during the hot growing season. Natural fires are most prevalent from April to early June, when high lightning frequencies often coincide with droughts (Komarek 1964, Myers 1990). Fires may substantially reduce canopy cover, and typically create extensive areas of bare ground (Chapter 2). Although convective thunderstorms are usually frequent for several months following natural fires, water is probably the limiting resource for recruitment; high soil surface temperatures, evaporation rates and infiltration rates may result in extremely hot, dry microsites for seedling establishment.

In this study I manipulated microsite litter, shade and soil water to mimic prefire and postfire conditions. I investigated the effects of microsite treatments on (1) abiotic conditions relevant to seed germination and seedling establishment at two times of year, and (2) seedling emergence and early establishment for two representative postfire-recruiting species in sand pine scrub.

I conducted the study using Eriogonum longifolium var. gnaphifolium (Polygonaceae; Reveal 1981) and Garberia heterophylla (Asteraceae), two relatively common, small-statured (< 2 m tall) perennial species (hereafter referred to by their generic names). I considered these species representative of sand pine scrub postfire recruiters because (1) both species resprout, flower, set seed and establish seedlings during the first year following fires; and (2) with the exception of sand pine (Pinus clausa), all immediate postfire recruiters in sand pine scrub are small-statured species.

Seeds of both Eriogonum and Garberia are nondormant; therefore, quantification of microsite effects on seedling establishment was expected to be relatively straightforward. Seed morphology and dispersal mechanism, however, differ between the species. Eriogonum produces propagules consisting of one seed attached to a persistent calyx; the propagules have no obvious seed dispersal mechanism, and typically drop beneath the parent plant (hereafter propagules will be called "seeds"). Garberia seeds have a pappus and are wind-dispersed. Eriogonum and Garberia seeds are identical in size (mean fresh mass = 3.7 ± 0.1 mg).

Timing of flowering, seed set and seedling establishment also differs between the species. Eriogonum flowering and seed set are rapid, with the majority of seedling establishment occurring during the summer following a fire. Flowering and seed set for Garberia, however, do not occur until December - January after a May - June fire, and seedling establishment occurs during the remainder of the winter and early spring following a fire (Chapter 2). Consequently, I conducted two separate experiments--one using Eriogonum seeds during the summer, and one using Garberia seeds during late winter - early spring.

In each experiment I quantified the effects of various combinations of litter, shade and supplemental watering on surface soil water content, surface soil temperature, and seedling emergence and early establishment. I expected surface soil water content to be the most important determinant of seedling establishment for both Eriogonum and Garberia. Consequently, in this study high levels of seedling establishment should be associated with high surface soil water content, and with treatment factors that result in high surface soil water content. Although litter, shade and supplemental watering all should increase soil water content, I expected supplemental watering and shade, and supplemental watering alone to be associated with highest surface soil water content during summer and winter, respectively.

Methods

Separate experiments were conducted using Eriogonum and Garberia seeds. The Eriogonum experiment was conducted during July and August 1993 in a sand pine scrub site at Archbold Biological Station in Highlands County, Florida, that was burned in May 1993. The Garberia experiment was conducted from January to March 1995 within a 0.25 ha cleared area at the Ocala National Forest Seed Orchard in Marion County, Florida. Each experiment was a 3 x 2 split-plot factorial design, replicated with 5 blocks. Shade was the whole-plot treatment, and litter and watering were subplot treatments within each shade treatment.

Eriogonum Experiment

A controlled burn was conducted at the Archbold Biological Station site on May 25, 1993. Most of the site was burned in strip head fires; the intense burn consumed most vegetation to a height of 2-3 m, and some leaves at heights up to 10-15 m. Less intense backfires burned strips of vegetation 10-30 m wide adjacent to fire breaks. The backfires consumed little vegetation above ground level.

In mid-July 1993, 40 circular metal rings, 10 cm in diameter and 9 cm high, were placed at the site, imbedded in the soil so that a vertical rim approximately 4.5 cm high protruded from the soil surface. Twenty Eriogonum seeds were placed within each ring; seeds were collected and bulked from approximately 150 plants at Archbold Biological Station. Each of the five experimental blocks consisted of eight combinations (each combination within one ring) of the following microsite conditions:

1. Shaded or unshaded- "Shaded" rings were placed beneath the relatively intact canopy of a back-burned area, while "unshaded" rings were placed nearby in an area consumed by a head fire. A spherical densiometer placed on the ground at the location of each ring was used to verify that the canopy above shaded microsites was < 20% open, and the canopy above unshaded microsites was > 40% open. Mean incident radiation (measured with an LI-188B Integrating Photometer; LI-COR, Inc.) for shaded microsites was 29.4 ± 9.0% that of unshaded microsites at the beginning of the experiment.

2. Litter or no litter- Litter treatments were randomly assigned to microsites, and litter was removed or added (using a combination of *Pinus clausa* and *Quercus* spp. litter collected elsewhere on the site) as needed so that the ground surface within each ring was either bare or completely covered with litter. Mean litter depth of the microsites with litter was 2.89 ± 0.3 cm. *Eriogonum* seeds were dropped on top of the litter, so some seeds may not have come into contact with the ground surface.

3. Watered or not watered- Watering treatments were randomly assigned to microsites. Approximately 380 ml of water was sprinkled on watered microsites during the evening (1830 or later) each day. This daily volume of water, equivalent to 4.8 cm of rain, was constrained by the amount of water that could be carried to the site. Both watered

and unwatered microsites received rainfall during the experiment.

Number of emerged seedlings was recorded daily, and each newly-emerged seedling was marked with a toothpick. A sample of approximately 30 cm^3 of soil was taken to a depth of 1 cm from the interior of each ring between 1400 and 1530 in late July 1993. Soil samples were weighed, dried for 24 hrs at 80 °C, and reweighed. Soil water content for each sample was expressed as a percentage of dry weight. Temperature of the top 1 cm of soil within each ring was measured with a mercury laboratory thermometer between 1300 and 1400 in early August 1993. Air temperature 2 cm above the ground was measured in representative shaded and unshaded microsites at the same time.

Records of daily rainfall and maximum and minimum air temperatures were obtained from the weather station at Archbold Biological Station. The weather station was approximately 1 km from the study site.

Garberia Experiment

In early January 1995, 40 circular plastic rings, 14 cm in diameter and 8 cm high, were arranged within a 4 x 5 m drip irrigation system grid. Twenty Garberia seeds were placed within each ring; seeds were collected and bulked from approximately 80 plants in Ocala National Forest and in Tiger Creek Preserve in Polk county. The irrigation grid consisted of 1.3 cm diameter hoses arranged as a central axis with five perpendicular branches. Each block of eight combinations of microsite conditions was located adjacent to a separate branch (Figure 4-1). The litter treatment was the same as used in the Eriogonum experiment, but methods used to create shaded and watered conditions differed, as noted below.

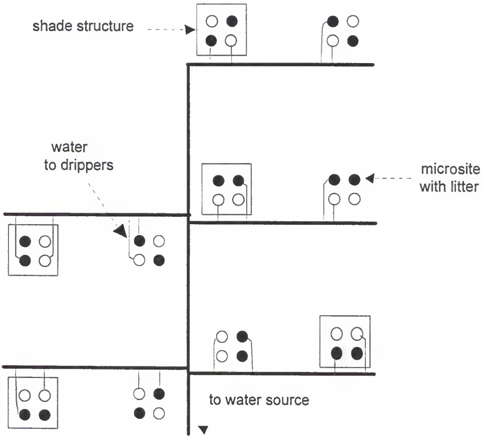


Figure 4-1. Arrangement of microsites within a drip irrigation grid for a seedling emergence experiment using Garberia heterophylla seeds, conducted January - March 1995. Treatments were applied to microsites using a split-plot factorial design, replicated with 5 blocks. Shade was the whole-unit treatment, and litter and watering were subunit treatments within each shade treatment.

Five shadecloth structures were constructed to provide shaded microsite conditions within each block. Each structure consisted of a 70 x 70 cm wooden frame, attached at the corners to four 60 cm wooden stakes. The entire 70 x 70 cm top and the upper 25 cm of the sides of each structure were covered with shade fabric (Weathashade Corporation) secured with staples. Shadecloth structures were positioned randomly within each block, and the stake "legs" of each structure were hammered into the soil until the top of the structure was 35 cm from the ground. Four rings were placed under the shadecloth structure in each block. Mean incident radiation (measured with an LI-188B Integrating Photometer; LI-COR, Inc.) for shaded microsites was 41 ± 4 % that of unshaded microsites.

Each randomly-chosen watered microsite received water via two low-volume drippers. Each dripper was mounted on a 0.6 cm diameter hose attached to the corresponding branch hose. Microsites were watered automatically from 0600 to 0615 daily; total water delivered daily to each microsite was approximately 3.5 l (equivalent to 22.7 cm of rain), determined by the capacity of the drippers.

Number of emerged seedlings was recorded weekly, and each newly-emerged seedling was marked with a toothpick. In late March 1995, soil and air temperatures were recorded and soil samples were collected as in the Eriogonum experiment. Percent soil water content was determined for each sample as in the Eriogonum experiment. Daily rainfall data were obtained from a weather station at the Ocala Seed Orchard, and records of daily maximum and minimum air temperatures were obtained from the Ocala Fire Control Center, approximately 32 km south of the study site.

Data Analysis

Differences in abiotic conditions and seedling emergence due to the treatment combinations were analyzed within each experiment using split-plot analyses of variance (SAS Institute Inc. 1988). Variables representing abiotic conditions were soil temperature and soil water content; total number of seedlings/experimental unit represented seedling emergence. Seedling data were converted to ranks prior to analysis.

Results

Eriogonum Experiment

Daily maximum and minimum temperatures remained relatively constant during the experiment (Figure 4-2); overall means and standard errors were 35.3 ± 0.2 $^{\circ}$C and 20.4 ± 0.2 $^{\circ}$C, respectively. Precipitation occurred on nine days during the 28 day experiment, and ranged from 0.05 cm to 3.26 cm (Figure 4-3).

During mid-afternoon in early August 1993, representative air temperatures at 2 cm above the ground for shaded and unshaded microsites were 38 $^{\circ}$C and 43 $^{\circ}$C, respectively. Mean soil temperatures ranged from 33.2 ±

0.7 °C in the shaded/no litter/watered microsites to 49.4 ± 1.9 °C in the unshaded/no litter/unwatered microsites. Mean soil temperatures were lower in shaded and watered microsites, and differed among blocks (Table 4-1, Figure 4-4).

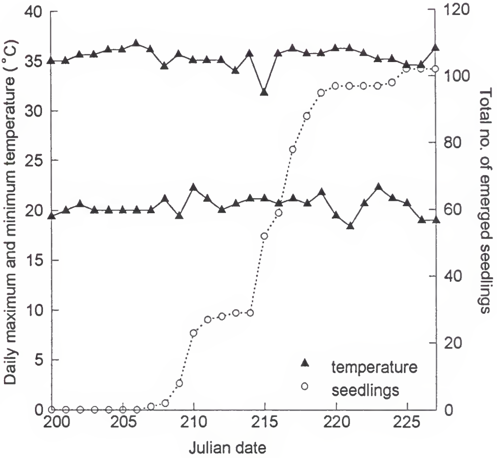


Figure 4-2. Maximum and minimum temperatures recorded during seedling emergence experiments conducted during July - August 1993 with Eriogonum longifolium var. gnaphifolium seeds. Temporal patterns of seedling emergence are also shown; 800 seeds were used in each experiment. Note differences in y-axis scales and labels.

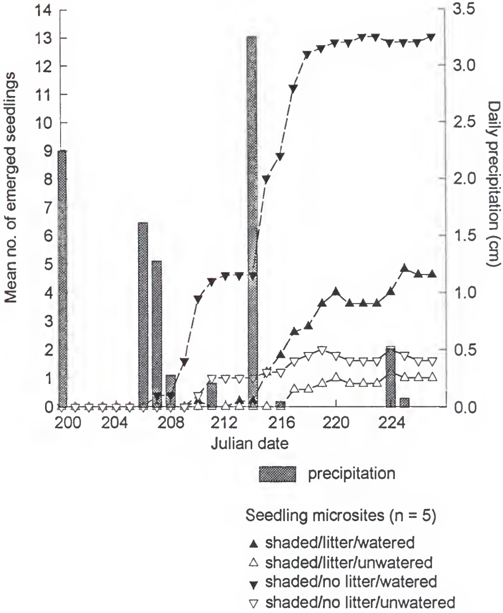


Figure 4-3. Seedling emergence patterns and precipitation recorded for experiments conducted during July - August 1993 with Eriogonum longifolium var. gnaphifolium seeds. Twenty seeds were used in each microsite treatment combination, created using shading, litter, and watering treatments. Note differences in y-axis scales and labels. Unshaded treatment results are not shown, as no seedlings emerged.

Table 4-1. P values from split-plot analyses of variance conducted on data for soil temperature and soil water content, and rank-transformed data for number of emerged seedlings. Data were collected from artificially constructed microsites during an experiment using *Eriogonum longifolium* var. *gnaphifolium* seeds in July - August 1993 (a) and during an experiment using *Garberia heterophylla* seeds in January - March 1995 (b). In each experiment shade was the whole-unit microsite treatment, and litter and watering were subunit treatments within each shade treatment.

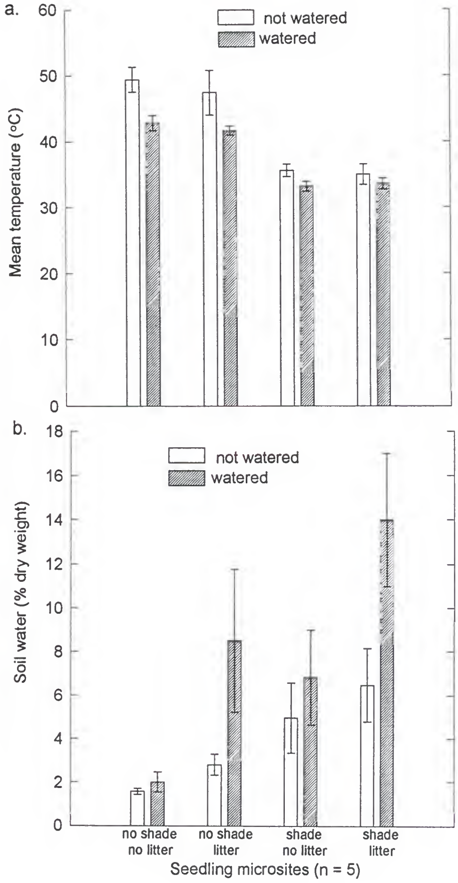
Source of Variation (Degrees of freedom)	Dependent Variable		
	Soil Temperature	Soil Water	Number of Seedlings
A. *Eriogonum* experiment			
block (4)	0.000	0.768	0.006
shade (1)	0.000	0.004	0.005
block * shade (4)	0.625	0.141	0.006
litter (1)	0.314	0.006	0.349
shade * litter (1)	0.373	0.863	0.349
water (1)	0.000	0.008	0.000
shade * water (1)	0.016	0.555	0.000
litter * water (1)	0.591	0.054	0.015
shade * litter * water (1)	0.952	0.938	0.015
B. *Garberia* experiment			
block (4)	0.016	0.223	0.626
shade (1)	0.000	0.500	0.692
block * shade (4)	0.140	0.373	0.009
litter (1)	0.031	0.195	0.927
shade * litter (1)	0.914	0.437	0.647
water (1)	0.000	0.000	0.000
shade * water (1)	0.000	0.402	0.070
litter * water (1)	0.007	0.183	0.454
shade * litter * water (1)	0.453	0.489	0.956

Mean percent soil moisture values calculated for samples collected on July 28 (12th day of experiment), three days after a rain, ranged from 1.58 ± 0.1% in unshaded/no litter/unwatered microsites to 13.98 ± 6.7% in shaded/litter/watered microsites. Shaded microsites, microsites with litter, and watered microsites had higher soil water contents (Table 4-1, Figure 4-4).

Emergence of Eriogonum seeds began seven days after sowing, and decreased substantially after 18 days. Pulses in numbers of emerged seedlings occurred following days with precipitation, primarily in shaded, watered microsites (Figure 4-3).

No seedlings emerged in unshaded microsites, while seedlings emerged from 15 of the 20 shaded microsites. Consequently, analysis of variance showed that the treatment factor "shade" as well as three of the four interactions that included shade accounted for significant portions of the variance (Table 4-1). Other important sources of variation were water and the interaction of litter with water (Table 4-1). More seedlings emerged in watered microsites than in unwatered microsites; this difference was accentuated in microsites with no litter (Figure 4-3). Shaded/no litter/watered microsites had the highest number of seedlings (mean ± S.E. = 13.0 ± 1.8).

Figure 4-4. Means and standard errors of (a) soil temperature and (b) percent soil water during a seedling emergence experiment using Eriogonum longifolium var. gnaphifolium seeds. Temperatures were recorded on August 8, 1993, from the top 1 cm of soil in the center of each microsite. Percent soil water was determined gravimetrically from samples collected on July 28, 1993. Each sample of approximately 30 cm^3 was collected from the top 1 cm of soil within the interior of a microsite.


a.
60
50
40
30
20
10
0
Mean temperature (°C)
not watered
watered
b.
18
16
14
12
10
8
6
4
2
0
Soil water (% dry weight)
not watered
watered
no shade
no litter
no shade
litter
shade
no litter
shade
litter
Seedling microsites (n = 5)

Garberia Experiment

Air temperatures decreased and then increased during the 12 weeks of this experiment. Weekly means of daily maximum and minimum temperatures ranged from 20.4 °C to 31.1 °C, and from 2.3 °C to 13.8 °C, respectively (Figure 4-5). Precipitation occurred on 13 days, during every week except the first, third, and last weeks of the experiment. Measurable daily precipitation varied from 0.26 cm to 3.0 cm, and measurable weekly totals varied from 0.33 cm to 4.08 cm (Figure 4-6).

In late March 1995, air temperatures at 2 cm above the ground for shaded and unshaded microsites were 34 °C and 39 °C, respectively. Mean soil temperatures ranged from 29.8 ± 0.7 °C in the shaded/no litter/watered and shaded/litter/watered microsites to 45.0 ± 0.5 °C in the unshaded/no litter/unwatered microsites. Soil temperatures were lower in shaded microsites, microsites with litter, and watered microsites. These temperature differences due to shade and litter were accentuated in watered microsites (Table 4-1, Figure 4-7).

Mean percent soil moisture values calculated for samples collected in late March ranged from 1.36 ± 0.05% in unshaded/no litter/ unwatered microsites to 14.26 ± 6.7% in unshaded/litter/watered microsites. Watered microsites had higher mean percent soil moisture values than unwatered microsites; no other treatment factors or combinations of factors had any effect on soil moisture (Table 4-1, Figure 4-7).

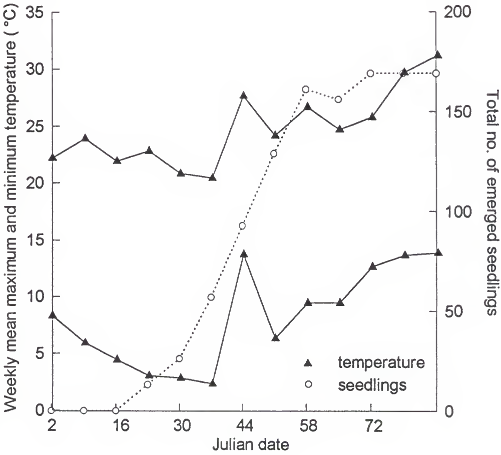


Figure 4-5. Maximum and minimum temperatures recorded during seedling emergence experiments conducted during January - March 1995 with Garberia heterophylla seeds. Patterns of seedling emergence are also shown; 800 seeds were used in each experiment. Note differences in y-axis scales and labels.

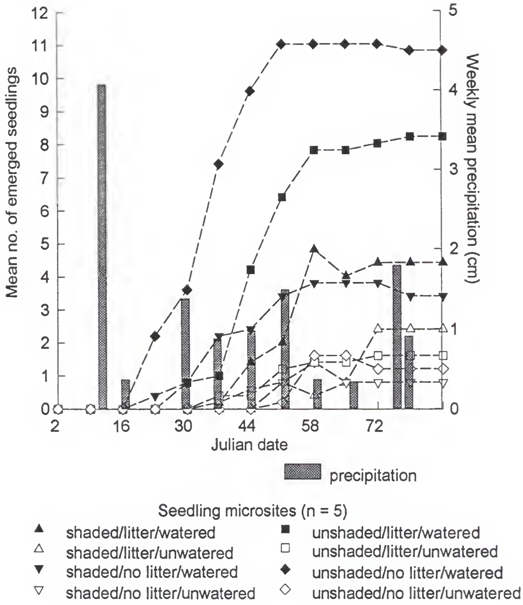
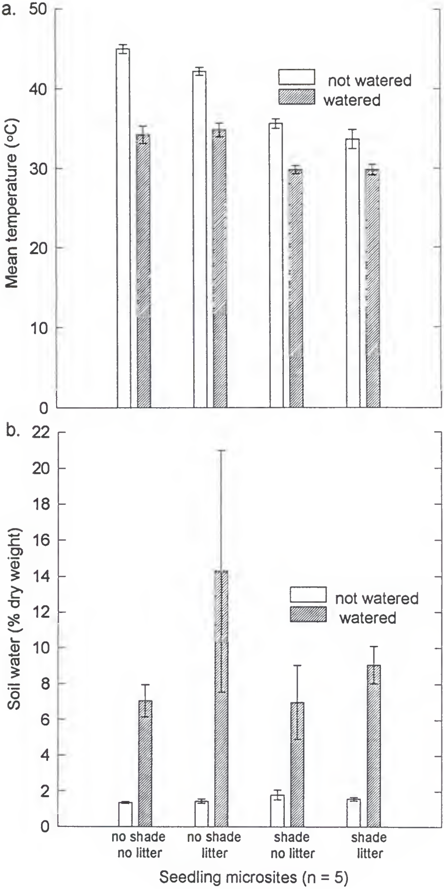


Figure 4-6. Seedling emergence patterns and precipitation recorded for experiments conducted during January - March 1995 with Garberia heterophylla seeds. Twenty seeds were used in each microsite treatment combination, created using shading, litter, and watering treatments. Note differences in y-axis scales and labels.

Figure 4-7. Means and standard errors of (a) soil temperature and (b) percent soil water during a seedling emergence experiment using Garberia heterophylla seeds. Temperatures were recorded on March 30, 1995, from the top 1 cm of soil in the center of each microsite. Percent soil water was determined gravimetrically from samples collected on the same day. Each sample of approximately 30 cm^3 was collected from the top 1 cm of soil within the interior of a microsite.


a.
Mean temperature (°C)
0
10
20
30
40
50
not watered
watered
b.
Soil water (% dry weight)
0
2
4
6
8
10
12
14
16
18
20
22
not watered
watered
no shade no litter
no shade litter
shade no litter
shade litter
Seedling microsites (n = 5)

Garberia seedlings were first detected four weeks after sowing, and number of seedlings increased until 11 weeks after sowing. Seedling emergence appeared to vary neither with weekly precipitation totals nor weekly mean air temperatures, although the highest seedling emergence rate occurred during a period of warmer temperatures (Figures 4-5 and 4-6). Seedlings emerged in all of the microsite treatment combinations, but only the shaded/no litter/watered, unshaded/litter/watered, and unshaded/no litter/watered microsites had seedlings in all replicates.

Watering was the only treatment that influenced seedling emergence; more seedlings emerged in watered microsites than in unwatered microsites (Table 4-1, Figure 4-6). Among the watered microsites, unshaded microsites tended to have more seedlings than shaded microsites, but this interaction failed to account for a significant amount of variation ($p = 0.07$). Unshaded/no litter/watered microsites had the highest number of seedlings (mean ± S.E. = 10.8 ± 3.4).

Seed predation was detected in neither experiment. Although ants occasionally entered the microsite rings, removal of seeds was never observed, and seeds did not "disappear" from microsites.

Discussion

Microsite Environmental Conditions

Similar experimental microsites resulted in sometimes extreme differences between the two experiments in abiotic conditions for seeds and seedlings. These differences, most likely due to dissimilar temperature regimes during the summer vs. winter - spring experiments, suggest that seasonal weather patterns may be as important as fire in modifying seedling microsites.

Under the high ambient temperatures of the summer *Eriogonum* experiment, water and shade were the treatment factors expected to have most influence on surface soil water content. While supplemental watering should increase soil water content, shade was expected to maintain high soil water content by reducing surface soil temperatures.

Shade and litter, however, were slightly more important than watering in maintaining high soil water content, indicating that water was being lost from the soil surface (probably through evaporation) during the experiment faster than it was being added through supplemental watering. Shaded microsites had lower soil temperatures than unshaded microsites, as expected, but soil temperatures were similar in microsites with and without litter. Rather than maintaining high soil water content through reducing soil temperature, litter probably created a high-humidity microenvironment or boundary layer above the soil surface, thereby reducing water loss (Facelli and Pickett 1991).

Not only did soil temperature influence soil water, but soil water appeared to influence soil surface temperature. Watered microsites had lower soil temperatures than unwatered microsites, especially when the microsites were unshaded. This temperature pattern can be attributed to the high specific heat and heat of evaporation for water, and suggests that surface soil water plays a role in moderating soil temperatures during the summer.

During the winter-spring Garberia experiment, watering was the most important influence on soil water content. As neither litter nor shading affected soil water contents, water apparently was not being lost from the soil surface at high rates as in the Eriogonum experiment.

Although shading and watering reduced soil temperatures as in the Eriogonum experiment, during the Garberia experiment litter also influenced soil temperatures. Temperatures were lower in microsites with litter, especially if the microsites were watered. In the relatively cool environment of this experiment, litter cover was sufficient to moderate soil temperatures, probably by both shading the soil surface and by physically impeding water loss (Facelli and Pickett 1991).

Seedling Emergence and Establishment

Seedling emergence and establishment of both species were expected to vary directly with soil water content. Given this prediction and differences in patterns and mechanisms relating to soil water content between the two experiments, *Eriogonum* emergence should have increased with shade, litter and watering, while *Garberia* emergence should have been influenced primarily by watering.
Although *Garberia* emergence varied with watering level as expected, *Eriogonum* emergence differed from the predicted pattern.

The lack of *Eriogonum* emergence in unshaded microsites cannot be completely explained by the environmental conditions measured in this study. The emergence pattern suggested that soil temperatures in unshaded microsites sometimes exceeded the range of favorable germination temperatures for this species; seedlings emerged relatively quickly in shaded microsites, with mean temperatures below 36 °C, but no seedlings emerged in unshaded microsites, with mean temperatures above 41 °C. A laboratory germination experiment conducted in conjunction with another study, however, demonstrated that exposure of *Eriogonum* seeds to 60 °C for 30 minutes did not decrease germination (Chapter 3). In addition, unshaded microsites tended to have drier surface soils than shaded microsites, but mean soil water of the unshaded/litter/watered microsites (in which no seedlings emerged) exceeded means for all of the shaded microsites except the shaded/litter/watered microsite type. Emergence may have failed in unshaded microsites due to either light inhibition of germination, or a combination of light inhibition and adverse effects of high temperatures and/or high light intensities. The degree of light inhibition of germination typically increases with light intensity, and also may increase with temperature (Bewley and Black 1994).

Another unexpected treatment effect on Eriogonum seedling emergence was the interaction between the litter and water treatments. In shaded, watered microsites, more seedlings emerged in microsites without litter than in those with litter. This pattern suggests that although soil temperatures and water contents were favorable for seedling germination and establishment, litter inhibited seedling establishment. Litter almost certainly acted as a mechanical barrier to seedling establishment, and also may have blocked light needed for establishment (Facelli and Pickett 1991, Vazquez-Yanes and Orozco-Segovia 1992). Some seeds on top of litter germinated and died before their roots could reach the soil surface. Seedlings from seeds that germinated underneath litter often were chlorotic and etiolated. Although apparently no similar studies have been conducted on other species in fire-influenced ecosystems, litter has been observed to inhibit seedling establishment in several early-successional species (Gross and Werner 1982, Goldberg and Werner 1983, Hamrick and Lee 1987).

In contrast, Garberia seedling emergence was not inhibited by litter, even though the seeds are the same size as Eriogonum seeds. Perhaps Garberia seedlings have a relatively low light requirement for successful establishment or their morphology facilitates emergence through litter; seedlings emerging from beneath litter generally appeared neither chlorotic nor etiolated, unlike Eriogonum seedlings. Alternatively, the more linear shape of Garberia seeds may enable them to more easily drop through litter to the ground surface. Although both Garberia and Eriogonum seeds were dropped on top of litter in the experiments, all Garberia seeds seemed to reach the ground surface, and germination on top of litter was never observed. In other studies, seed and seedling morphologies apparently facilitated seedling establishment in the presence of litter (Grime 1979, Gross and Werner 1982, Facelli and Pickett 1991).

Also in contrast to Eriogonum, high temperatures did not influence Garberia seedling emergence. Air temperatures during part of the Garberia experiment, however, may have been at the low end of favorable germination temperatures for the species. Even though in laboratory experiments Eriogonum and Garberia germinated over similar lengths of time (germination occurred for 1 - 2 weeks, initiating 3 - 4 days after sowing; unpublished data), Garberia seedlings in this study emerged over a much longer period of time, with the highest emergence rate occurring during a period of warming temperatures. The weak trend among watered microsites of fewer seedlings germinating in shaded than in unshaded microsites also may have been due to low soil temperatures; mean soil temperatures in shaded, watered microsites were lower than those in other microsite types. The artificial shade structures used in this experiment, however, were less effective at excluding light and lowering soil temperatures than the natural canopy in the *Eriogonum* experiment. Perhaps if the shade structures had simulated a natural canopy more closely, seedling emergence would have differed between shaded and unshaded microsites.

Watering treatments also differed between the experiments; *Garberia* seeds received the equivalent of 22.7 cm of rainfall daily, while *Eriogonum* seeds received the equivalent of 4.8 cm of rain. Although this difference in watering treatments was not reflected in measured soil water contents, the pulses in *Eriogonum* seedling emergence following precipitation events suggest that seedling establishment was somewhat water-limited even in watered microsites. Although the watering treatment alone probably resulted in water imbibition by seeds and some seedling emergence, supplemental water from precipitation apparently offset water loss from the soil surface so that many of the seeds could complete germination and early establishment.

Relevance of Experimental Microsites to Postfire Recruitment in Sand Pine Scrub

A previous study has shown that although fires in sand pine scrub reduce mean litter depths and enlarge canopy openings, burned sites may retain some pre-fire patterns of microsite conditions, particularly litter depth patterns (Chapter 2). Differences in litter depths, when combined with heterogeneous light conditions and overlain with temporal differences in air temperature and precipitation, form an intricate variety of microsite conditions for postfire seedling recruitment. Studies conducted in other fire-influenced ecosystems have shown that recruitment success of different species varies among postfire microsites (Lamont et al. 1993), and also varies between prefire and postfire microsites (Christensen and Muller 1975, Wellington and Noble 1985).

The short-term experiments in this study measured only early seedling establishment, and not long-term seedling survival needed for completion of recruitment. Also, the experimental microsites were simplistic examples of conditions for seeds and seedlings in burned and unburned sites, as only extreme, or endpoint conditions were represented. Nevertheless, this study not only showed that abiotic conditions are harsh for seedling establishment, particularly during summer, but also suggested that tradeoffs in environmental conditions for seedling recruitment exist between different seasons within the first year after fire. During the first one to four months following typical growing season fires, extensive areas of bare soil and increased light availability at the ground level may benefit recruitment, but seeds and seedlings also must contend with high, potentially lethal soil temperatures and accelerated loss of water from the soil surface. Later, during winter and spring, soil temperatures and rates of soil water loss are lower, but accumulated litter, low soil temperatures, and/or sparse precipitation may delay or inhibit seedling establishment.

More specifically, litter can have contrasting effects on seedling establishment in relation to fires. This study has shown that accumulations of litter typical in the absence of fire can be detrimental to seedling establishment of species such as Eriogonum; moreover, other studies have suggested that allelopathic leachates from litter of some Florida sand pine scrub species inhibit seedling establishment (Richardson and Williamson 1988, Fischer et al. 1994). In open microsites common immediately after fires, however, unburned or partially consumed litter may retard water loss from surface soils after often light, sporadic summer rains. These relatively mesic microsites may facilitate seedling establishment of some species.

Although litter can retard water loss from surface soils and under some conditions can moderate soil surface temperatures, shading resulted in the highest soil water contents and the lowest soil temperatures during the summer

Eriogonum experiment. Consequently, the most favorable microsites for seedling establishment during summer months following fires should be in shaded microsites. Individuals or groups of shrubs and small trees provide shaded microsites and potentially function as "nurse plants" (sensu Turner et al. 1966), particularly after patchy or relatively low-intensity burns.

Although seedlings of some species such as Eriogonum manage to establish during summers after fires beneath nurse plants or in other relatively mesic microsites, most sand pine scrub species apparently recruit primarily during the first winter to spring after a fire. Within the first year following a sand pine scrub May 1993 fire, seedlings of only four plant species established during July. Seedlings of 18 species were detected at the same site in March, however, and 16 seedling species were detected in January at another site also burned in May 1993. Numbers of newly-established seedlings also peaked during winter and spring during the first year postfire at the two sites (Chapter 2). Studies in Florida sandhill (Whelan 1985) and Australian scrub heath (Enright and Lamont 1989) also showed that most recruitment occurred several months after fire during cooler weather.

The results of this study suggest that Eriogonum and Garberia have different postfire regeneration niches (sensu Grubb 1977), as has been demonstrated for plant species in some other communities (Gross and Werner 1982, Goldberg and Werner 1983, Fowler 1988). Characteristics of Garberia seeds and seedlings seemed to compensate for greater litter depths that may occur with increasing time after fire, since seedlings established equally well in microsites with and without litter. Like Garberia seedlings, seedlings of other sand pine scrub species that recruit during the winter and spring following growing season fires also may be capable of establishing under a relatively wide range of microsite conditions.

Eriogonum seedlings, in contrast, appeared to establish under a narrow range of environmental conditions. As one of only four species that recruited during the first summer after the May 1993 fire, its seedlings may be at a disadvantage in establishing with increasing time after fire. Specifically, Eriogonum recruitment may decrease with increased litter depths and decreased light availability. Although not addressed in this study, belowground competition also might be an impediment to seedling establishment with increasing time after fire. Postfire seedling establishment appears to be rare for this species (Chapter 2), probably because physical microsite conditions favorable to establishment coincide with extremely harsh temperature, insolation and soil moisture conditions; virtually no recruitment occurs in the absence of fires (Chapter 2). Most recruitment apparently occurs when fires are followed by above-average precipitation during the summer.

Additional research on regeneration characteristics (e.g., seed size and shape, germination requirements, seedling establishment requirements) of species that recruit during different seasons following fire is needed to determine if generalizations can be made concerning the relationship of postfire recruitment characteristics to seasonally changing microsite conditions in sand pine scrub. Also, research in other pyrogenic ecosystems might determine whether different soil characteristics or climatic patterns influence regeneration characteristics.

CHAPTER 5

SOIL SEED BANK STRUCTURE AND COMPOSITION IN FLORIDA SAND PINE SCRUB

Introduction

The importance of seed banks in community dynamics has been demonstrated for some fire-influenced communities, such as California chaparral (Zammit and Zedler 1994). Although woody perennials that resprout quickly after fire often are prominent in California chaparral (Keeley and Zedler 1978), postfire regeneration is characterized by a large flush of seedling germination (Christensen and Muller 1975). Seedlings are primarily annuals, but may include resprouting and obligately-seeding (i.e., incapable of resprouting) shrub species. Annual species that comprise the majority of postfire seedling germination may persist as dormant seeds for several decades, and may be rare or absent as adult plants in long unburned areas.

In this paper I report the results of a community-level study of the seed bank in Florida sand pine scrub, a community with physiognomy, fire frequency and fire intensity similar to those of California chaparral. The objectives of the study included quantification of a seed bank for herbaceous and partially woody dicotyledonous species, and herbaceous monocotyledonous species (hereafter "herbaceous plants") in sites differing in time since last fire. Presence of a seed bank would suggest that postfire seedling establishment is a component of life histories for herbaceous and suffrutescent plant species in Florida sand pine scrub.

Sand pine scrub is a shrubby community found primarily in Florida on well-drained, sandy, low-nutrient soils (Myers 1990). The community is dominated by several species of sclerophyllous clonal oaks (Quercus spp.), often with sand pine (Pinus clausa) prevalent in the overstory. Herbaceous plants are usually present in low numbers but become more obvious after infrequent fires or other disturbances (Myers 1990, Greenberg et al. 1995). Sand pine scrub patches in inland peninsular Florida typically burn every 10 to 100 years and are often surrounded by more frequently burned pinelands such as longleaf pine (Pinus palustris)- wiregrass (Aristida beyrichiana) sandhills (Myers 1990); the numerous scrub "islands" in Florida are thought to be remnants of a more widespread plant association dating back to the Miocene epoch (Webb 1990). Presumably as a result of its history as isolated habitat patches, sand pine scrub now supports 19 endemic plant species--more than any other plant community in Florida (Christman 1988, Myers 1990). Little detailed information exists on the life histories and ecology of most of these woody and herbaceous plant species.

A recent plant community study, however, has shed some light on general life history characteristics with respect to fire for several species found in sand pine scrub (Menges and Kohfeldt 1995). Most of the plant species studied persisted through fires via one of four life history strategies. Most species occurring in sand pine scrub were classified as "resprouters" and "resprouters and clonal spreaders;" these two groups include oaks and other woody shrubs that regenerate rapidly after fire from persistent roots and rhizomes. Most small-statured (< 2 m tall) herbaceous and woody species, however, were considered "resprouters and seeders" and "obligate seeders." Postfire seedling establishment occurs in both of these groups of plants, and while infrequent seedling establishment may help to ensure longterm population persistence for "resprouters and seeders," "obligate seeders" depend on seedling establishment after every fire or comparable disturbance to avoid extirpation.

For species incapable of resprouting after fire, seeds in a persistent seed bank should have a significant contribution to population dynamics. A persistent soil seed bank has been shown to be integral to the demography of _Ceratiola_ _ericoides_ (Empetraceae), a common obligately-seeding shrub in sand pine scrub (Johnson 1982). Seed banks must be essential for persistence of other obligately seeding species, and also may exist for some "resprouters and seeders." Quantification of the composition and dynamics of sand pine scrub seed banks should contribute to an understanding of community-level responses to fire, especially if comparisons among data on seed banks and adult plants indicate that underground and aboveground processes differ.

The existence of seed banks in many communities is tied to natural disturbances, as germination requirements are often met only by postdisturbance conditions. Even though some seeds (particularly of short-lived species) must be capable of surviving from one disturbance to the next, in most seed bank studies researchers have monitored germination from soil samples for only a few years at most (e.g., Schneider 1988, Zammit and Zedler 1994), and have not related seed longevity to natural disturbance frequency. Understandably, the long time required to quantify seed longevity in relation to natural disturbance frequency is usually prohibitive.

In this study I investigated the existence of a persistent seed bank in sand pine scrub by quantifying viable soil seed densities in relation to adult plant densities at sites differing in time since last fire. The study was based on the hypothesis that seeds in a seed bank should persist longer after fire than adult plants, due to seed densities declining more slowly over time than adult plant densities (Noble and Slatyer 1980). I predicted that differences in soil seed densities of herbaceous species between recently burned and long unburned sites should be smaller than differences in densities of adult herbaceous plants at the same sites. For relatively long-lived species, seed bank species composition should be similar to adult plant species composition at a given site. In addition, occurrences of species of seeds in the soil should be correlated with occurrences of conspecific adult plants, since adult herbaceous plants often are sparse even after fires, and many seeds have no obvious dispersal mechanisms. Other, shorter-lived species present as seeds in seed banks might be absent from sites as adults. I quantified abundances, species composition, and distributions of seeds in the soil and of adult plants to test these predictions.

Methods

Soil samples were collected from three recently burned and five long unburned sand pine scrub sites. One recently burned site, at Archbold Biological Station (hereafter "Archbold") in Highlands County, Florida (27° 15', 81° 15'), had burned one year previously. The other two recently burned sites burned two years before soil collection in separate fires, and were located at Saddleblanket Lakes Preserve (hereafter "Saddleblanket") in Polk County, Florida (27° 45', 81° 45'). All of the long unburned sites had not burned in at least 40 years; three were located at Archbold and two were in Ocala National Forest (hereafter "Ocala") in Marion County, Florida (29° 0', 81° 45').

Soil samples were collected from the four Archbold sites during August 1992, and were collected from the remaining sites during December 1992. At each site soil samples were collected within 1 m^2 plots positioned at stratified random intervals up to 10 m away from alternating sides of a 100 m transect; samples were collected from 33 plots at each site. Transects were located at least 100 m away from an access road, and oriented randomly while avoiding edges and disturbed areas. Each soil collection plot was located a random perpendicular distance from the transect. If herbaceous plants were present at a selected distance along the transect and within 10 m of either side of the transect, however, the plot was shifted perpendicular to the transect until the plot included at least one adult herbaceous plant. This modification in sampling was necessary because (1) herbaceous plant density was often very low; (2) seeds and fruits of many herbaceous species in sand pine scrub have no obvious dispersal mechanisms; and (3) preliminary sampling revealed that seeds from herbaceous plants in the soil were sparse, patchily distributed, and virtually absent in areas of dense growth of oaks and other clonal species.

Within a 1 m^2 soil collection plot, stems were counted for all species of dicotyledonous herbaceous plants (all non-clonal), and an ocular estimate was made of percent cover of all species of grasses, sedges, and oaks and other woody species.

To estimate buried seed densities, two soil subsamples were taken within each 1 m^2 plot, and then combined. Each subsample consisted of five soil cores 2.5 cm in diameter x

5 cm deep collected within a randomly selected 20 cm^2 area (Gross 1990). Ninety percent of each composited soil sample was spread to a thickness of 1 cm in a germination flat immediately after collection, the germination flats were placed in greenhouses, and germinating seedlings were counted and identified. Soil samples were monitored in two greenhouses due to space and time constraints. Samples from the Archbold sites were placed in an unheated greenhouse at Archbold Biological Station and watered daily from August 1992 to January 1993. The samples were checked monthly for germinating seeds. All other soil samples were placed in a greenhouse at the University of Florida kept at approximately 24 °C and watered daily. Samples were checked weekly for germinating seedlings from December 1992 to April 1993. Seeds were extracted from the remaining 10% of each soil sample by sieving, to determine if seeds $\geq$ 1 mm diameter not detected by germination were present in soil samples (seeds < 1 mm in diameter were too small to be separated from soil by sieving).

Number of germinating seeds, stem densities of dicotyledonous herbaceous plants, and percent cover of grasses and sedges were compared between recently burned sites and long unburned sites using Mann-Whitney U tests. Distributions of seeds in the soil and adult herbaceous plants were compared using chi-square tests.

Results

A total of 502 seedlings germinated from soil samples collected, and 77% were identified to 10 species and/or genera (Table 5-1). Buried seed densities were low in most sites; in two long unburned Archbold sites, the recently burned Archbold site and one long unburned Ocala site the median seed density was 0 seedlings/m^2 (Table 5-2). The two recently burned Saddleblanket sites had the highest densities of buried seeds, with medians of 122 seedlings/m^2 and 204 seedlings/m^2. The median density over all sites was 20 seedlings/m^2. Although soil samples from recently burned sites tended to have higher buried seed densities, the densities were not significantly different between recently burned and long unburned sites (Mann-Whitney U test, $p > 0.1$). Sieving yielded no species of seeds in addition to those detected by germination from soil samples.

Stem densities of dicotyledonous herbaceous plants were higher in recently burned sites than in long unburned sites (Mann-Whitney U test, $p < 0.05$); the highest median density in a recently burned site was 2 stems/m^2 (Table 5-3). Percent cover of grasses and sedges and percent open canopy were low in all sites, with no differences between the two types of sites (Mann-Whitney U test, $p > 0.1$) (Table 5-3).

Species composition of seeds from the soil samples (as detected by germination) was similar between long unburned and recently burned sites, with the common taxa present in both types of sites (Table 5-1). Species compositions of

Table 5-1. Species and numbers of seedlings germinating from soil samples collected at five long unburned and three recently burned Florida sand pine scrub sites, August - December 1992. Patterns of seed and adult occurrence in soil samples, and growth form are in parentheses.

Species	Sites[a]							
	Unburned					Burned		
	A1	A2	A3	O1	O2	A4	S1	S2
Cyperus spp. (s+a[b], p[c])	3	1	5	28	3	2	67	145
Linaria floridana (s, a)	1	4	7			4	7	30
Rhynchospora megalocarpa (s+a, p)			1	7		26		
Dicanthelium spp. (s+a, p)		4	2		2	1		6
Eupatorium spp. (s, wp)		2	3	5	4		3	4
Physalis spp. (s, wp)		1	1					4
Conyza canadensis (s, wa)		1	1		1			
Stipulicida setacea (s, p)							4	5
Palafoxia feayi (s, p)		1						
Lyonia ferruginea (s, p)			1					
unknown grasses		4				3	4	8
unknown monocotyledonous spp.				1				
unknown dicotyledonous spp.	4	4	4	14	4	2	24	35
unknown	1	2	7			1		4

[a] Site codes: A1 - A4 = Archbold 1 - 4; O1, O2 = Ocala 1, 2; S1, S2 = Saddleblanket 1, 2

[b] s = seeds present; a = adults present

[c] p = perennial; a = annual; w = weedy

Table 5-2. Numbers of soil samples with germinated seeds, and seed density medians and ranges from five long unburned and three recently burned Florida sand pine scrub sites.

Site	# samples with seeds (*n* = 33)	Seeds/m^2 (median and range)
A. Long unburned sites[a]		
Archbold 1	6	0 (0 - 82)
Archbold 2	11	0 (0 - 163)
Archbold 3	21	41 (0 - 122)
Ocala 1	17	41 (0 - 774)
Ocala 2	12	0 (0 - 163)
B. Recently burned sites		
Archbold 4	8	0 (0 - 122)
Saddleblanket 1	28	122 (0 - 774)
Saddleblanket 2	29	204 (0 - 1385)

[a] Mann-Whitney U test showed no difference in seed densities between long unburned sites and recently burned sites ($p > 0.1$).

seedlings from soil samples, compared to the species compositions of adult plants from plots where soil samples were collected, however, were dissimilar at all sites for dicotyledonous species. Adults of most dicotyledonous species represented in the seed banks were absent from the sites; only Palafoxia feayi and Linaria floridana were found within sample plots. Of 55 seed occurrences in sample plots, conspecific adults never occurred in the same plots (chi-square test, $p < 0.005$). Monocotyledonous species, however, were generally present both as seeds and as adults. Of 81 seed occurrences in sample plots, a conspecific adult was present in 35 cases (chi-square test, $0.1 < p < 0.25$).

Table 5-3. Medians and ranges of herbaceous plant stem densities and percent cover values in long unburned and recently burned Florida sand pine scrub sites.

Site	# Stems/m^2 of herbaceous dicotyledonous species	% Cover of grasses and sedges
A. Long unburned sites		
Archbold 1	1 (0 - 5)	0 (0 - 25)
Archbold 2	0 (0 - 3)	0 (0 - 10)
Archbold 3	0 (0 - 2)	0 (0 - 10)
Ocala 1	0 (0 - 2)	0 (0 - 20)
Ocala 2	0 (0 - 2)	5 (0 - 20)
B. Recently burned sites[a]		
Archbold 4	1 (0 - 8)	0 (0 - 10)
Saddleblanket 1	2 (0 - 8)	10 (0 - 30)
Saddleblanket 2	1 (0 - 5)	5 (0 - 30)

[a] Recently burned sites had higher stem densities of dicotyledonous species than long unburned sites (Mann-Whitney U test, $p < 0.05$).

Discussion

By characterizing seed bank size and structure for Florida sand pine scrub, this study adds to a small number of similar community-level seed bank studies in fire-influenced communities (Hassan and West 1986, Schneider 1988, Zammit and Zedler 1994). The sand pine scrub seed bank in this study, with 20 seeds/m^2 representing 10 taxa (as quantified from germinating seeds), is small compared to seed banks in California chaparral (Zammit and Zedler 1994), but is similar to numbers reported for sagebrush semidesert in Utah (Hassan and West 1986) and pine-wiregrass savanna in North Carolina (Schneider 1988; Table 5-5).

Table 5-4. Herbaceous plant species occurring as adults in at least 2 plots/site in long unburned and recently burned Florida sand pine scrub sites.

Species	Sites[a]							
	Unburned					Burned		
	A1	A2	A3	O1	O2	A4	S1	S2
Andropogon virginicus							x	x
Aristida beyrichiana	x							
Calamintha ashei	x							
Ceratiola ericoides					x			
Chapmannia floridana	x	x	x			x		
Conradina brevifolia							x	x
Cyperus spp.						x	x	
Eriogonum longifolium var. *gnaphifolium*	x							
Garberia fruticosa				x	x			x
Liatris tenuifolia					x			
Palafoxia feayi		x	x			x	x	x
Rhynchospora megalocarpa			x	x	x			

[a] Site codes: A1 - A4 = Archbold 1 - 4; O1, O2 = Ocala 1, 2; S1, S2 = Saddleblanket 1, 2

Table 5-5. A summary of seed bank densities and structures in pyrogenic communities.

Community	Seed bank size ($seeds/m^2$)	Seed bank structure (# species)	Total # species
Sand Pine Scrub (this study)[a]	20	3 monocot perennials 5 dicot perennials 2 annuals	10
Pine-wiregrass Savanna (Schneider 1988)[a]	not reported	6 monocot perennials 10 dicot perennials 2 annuals	18
Sagebrush Semidesert (Hassan and West 1986)[b]	3.3 - 91.5	5 monocot perennials 11 dicot perennials 5 annuals	21
Chaparral (Zammit and Zedler 1994)[a]	3280 - 7830	1 monocot perennial 9 dicot perennials 42 annuals	52

[a] soil seed density quantified by monitoring germination
[b] soil seed density quantified by sieving

Although the method of locating soil sample plots presumably biased this study towards finding seeds, the reported seed bank density for sand pine scrub may be an underestimate. The seedling emergence method of seed bank quantification inherently underestimates densities of viable seeds in the soil, as conditions for germination may not be met for some seeds (Simpson et al. 1989). Given the limitations of the method, more frequent monitoring of germination, a longer period of monitoring, and spreading soil samples more thinly in germination flats (Dalling et al. 1995) could have resulted in a larger density estimate. Because seed bank sizes among fire-influenced communities vary by orders of magnitude, however, a more accurate estimate of seed bank size probably would not affect the comparisons discussed above.

Sand Pine Scrub Seed Bank Components

The seed bank in sand pine scrub appears to consist of three seed bank components, corresponding to different combinations of seed occurrence and conspecific adult occurrence in soil samples. The component consisting of monocotyledonous species had the largest number of seeds, and was the only group in which conspecific adults were present in the same sample plots as their seeds (Table 5-1). Species with this pattern of seed and adult occurrence are associated with one or a combination of the following characteristics:

1. adults may be short-lived, but continually produce seeds and recruit new individuals between fires
2. recruitment occurs primarily after fires, from resprouting, long-lived adults

The second sand pine scrub seed bank component is comprised of "weedy" species (e.g., _Eupatorium_ spp., _Physalis_ spp., _Conyza_ _canadensis_) present only as seeds in the study sites (Table 5-1). Like many other weeds, species in this group have good long-distance seed dispersal, and probably dispersed into the sites from adjacent areas with disturbed soil. Although these species comprised the second largest number of seeds identified in soil samples, adults are rarely present in sand pine scrub after fires (Schmalzer and Hinkle 1992, personal observations), and are absent in sand pine scrub under a natural fire regime.

The third seed bank component consists of species with poor seed dispersal that were generally present as seeds but not as plants (Table 5-1); Linaria floridana and Stipulicida setacea are representative species. Linaria floridana is an annual species with very small seeds (~ 0.5 mm diam.) lacking an obvious dispersal mechanism; in this study it was represented by seeds in six sites and by adult plants in only one recently burned site. This species must depend on seeds accumulated in a persistent seed bank to maintain populations between disturbances. Stipulicida setacea is an annual or short-lived perennial that, like Linaria, has very small seeds (< 0.5 mm diam.) without an obvious dispersal mechanism. This species was represented by seeds but never as adults in the sample plots; however, it was occasionally present in the study sites.

Several species that were present as adults in sample plots were not represented in the seed bank. Seeds were not detected for Ceratiola ericoides and Calamintha ashei, two "obligate seeders" (Johnson 1982, Menges and Kohfeldt 1995) expected to have seed banks, and present as adults in sample plots. Seeds of these species may have been dormant and not stimulated to germinate; although seeds of both species are > 1 mm in diameter, they may have been present at such low densities in the soil that they were missed by sieving. Seeds of several other dicotyledonous species present as adults on study sites were detected neither by germination nor by sieving, although lower densities of adults on long unburned sites suggests that adults of some species are short-lived and rely on long-lived seeds to persist between fires.

Comparisons with Other Pyrogenic Communities

Pine-wiregrass savanna and sagebrush semidesert are similar to sand pine scrub in seed bank size and structure (Table 5-5). Seed banks in all three communities are sparse, and consist largely of perennials. Conversely, annual species represent a disproportionately large proportion of the much larger California chaparral seed banks, and monocotyledonous perennials are virtually absent (Table 5-5).

I suggest that a fundamental difference in community response to disturbance underlies the discrepancy between chaparral seed banks and seed banks in sand pine scrub, pine-wiregrass savanna, and sagebrush semidesert. Grubb (1988) hypothesized that species in communities with dense vegetation cover have seedling recruitment tightly coupled with disturbance events; seed banks of these species are largely persistent, with seed dormancy broken by cues associated with disturbance. Species in communities with less shading have recruitment relatively uncoupled with disturbance events, seed banks variable over time and sometimes small, and variable seed dormancy mechanisms.

Going from species-level recruitment to community-level recruitment and assuming that seedling recruitment (and associated seed bank dynamics) in each fire-prone community falls somewhere on a gradient between being "coupled" and "uncoupled" (sensu Grubb 1988) with disturbance, California chaparral is more consistent with "coupled" recruitment. In comparison, seed bank size and structure in Florida sand pine scrub are more consistent with "uncoupled" recruitment, as are seed banks in pine-wiregrass savanna and sagebrush semidesert.

Whereas the shrub layer of unburned chaparral is very dense and the majority of herbaceous species recruitment occurs after fires, mature pine-wiregrass savanna and sagebrush semidesert are relatively open, and seedling recruitment tends to be less tightly associated with fires. The shrub layer in mature sand pine scrub can vary from dense to relatively open, but as in pine-wiregrass savanna and sagebrush semidesert, seedling recruitment is not strongly associated with fires (Chapters 2, 6).

Although size and structure of the sand pine scrub seed bank is consistent with recruitment "uncoupled" to disturbance, the determination of seed bank persistence in this study was inconclusive. With a persistent seed bank, differences in herbaceous plant abundances between recently burned and long unburned sites were expected to be larger than differences in seed bank densities. The lack of difference detected between seed bank densities from the two treatment groups suggests that monocotyledonous species (with no difference in adult abundances) have transient seed banks and dicotyledonous species (with smaller adult densities in long unburned sites) have persistent seed banks. These results are suspect, however, because inconsistencies in methodology are partially responsible for the failure to detect a difference in seed bank densities between recently burned and long unburned sites. Variation among collection dates for soil samples and variation in greenhouse conditions for germination increased within-treatment variation in seed density estimates. Consequently, detection of a difference in seed densities between recently burned and long unburned sites was unlikely.

Longer-term community or single species studies are required to quantify seed longevities and/or fluctuations in seed bank densities. Since seed banks have been quantified for "obligate seeders" in sand pine scrub and in other fire-prone communities (Keeley 1977, Johnson 1982, Keeley 1987), intensive soil sampling under adult obligately seeding plants should be done to detect low numbers of seeds in the soil.

To better understand the general dynamics of plant species recruitment and survival after and between fires in sand pine scrub, future research should concentrate on conditions needed for growth, resprouting, and seedling establishment for species represented in the seed bank as well as for those that are absent. Knowledge gained from such research may lead to implementation of fire regimes and/or mechanical treatments better suited to the life history characteristics of these species.

CHAPTER 6

SEEDLING RECRUITMENT PATTERNS IN RELATION TO SITE CHARACTERISTICS IN FLORIDA AND CALIFORNIA FIRE-INFLUENCED COMMUNITIES

Introduction

Natural fires occur in virtually all terrestrial ecosystems on earth with varying predictability, frequency and intensity (e.g., Whelan 1994). Concomitantly, the role of fire as a disturbance varies among ecosystems. At opposite ends of the disturbance spectrum are unpredictable, extremely infrequent fires that function as catastrophic disturbances in tropical rainforests (Mueller-Dombois and Goldammer 1990), and predictable fires that influence plant species life history characteristics and maintain plant species diversity in Mediterranean-climate ecosystems (Christensen 1985, Keeley 1986).

Mediterranean-climate ecosystems and other ecosystems such as boreal forests are considered "fire-adapted" because their plant species have a variety of characteristics that allow them to survive or recover from fires. Although many species in these ecosystems have traits such as resprouting from underground structures and thick bark that increase their resilience to fire, traits such as obligate seeding (i.e., establishing seedlings after adults are killed by fire), stimulation of seed germination by heat or smoke from fire, and serotinous cones or fruits are more likely specific adaptations to fire (Wells 1969, Gill 1981, Barbour and Minnich 1990, Johnson 1992).

In species with heat- or smoke-induced germination; serotiny; seedling establishment after adults are killed by fire (i.e., "obligate seeding;" Naveh 1975); and seedling establishment from resprouting, flowering adults; seedling recruitment is "coupled" (sensu Grubb 1988) to fire as a disturbance. Natural fires are essential in maintaining species composition in communities with large proportions of these postfire-recruiting species. Although postfire species recruitment presumably evolves in response to good conditions for survival after fires relative to conditions before fires, recruitment characteristics are additionally influenced at the species and community levels by the fire regime (e.g., fire frequency, intensity and season) and by abiotic site characteristics (e.g., rainfall abundance and seasonal pattern, soil texture and nutrient status) at various spatial scales (see Chapter 4).

Most comparisons between geographic regions of postfire recruitment characteristics have involved Mediterranean-climate communities in California, Chile, the Mediterranean basin, southern Australia and South Africa. In these comparisons, importance of recruitment traits such as postfire flushes of annual herbs, serotiny and heat- or smoke-induced germination generally has varied among regions with soil nutrient status and anthropogenic disturbance regime (Cody and Mooney 1978, Naveh and Whittaker 1979, Shmida 1981, Barbour and Minnich 1990).

In Australian and South African communities with very old, nutrient-poor soils, serotiny and heat- or smoke-induced germination are prevalent traits, but annual species are scarce and not conspicuous after fires (Specht 1969, Cody and Mooney 1978, Barbour and Minnich 1990, Le Maitre and Midgley 1992). Communities in California, Chile and the Mediterranean basin, however, are associated with comparatively young, nutrient-rich soils (Specht 1969, Hanes 1981). Although many annual species occur in the communities of all three regions (Rundel 1981, Shmida 1981, Keeley and Keeley 1988), only California has significant postfire flushes of annuals; serotiny and heat- or smoke-induced germination also are prevalent only in California (Cody and Mooney 1978, Barbour and Minnich 1990). Researchers have suggested that scarcity of these recruitment characteristics in Chile and the Mediterranean basin is a result of the intensity and long length of time of human disturbance in both regions (Keeley and Johnson 1977, Cody and Mooney 1978, Naveh and Whittaker 1979).

At the regional scale, both the fire regime and site characteristics may influence postfire recruitment, and trends in biotic and abiotic characteristics of ecosystems may differ from trends at the global scale. Infrequent, intense fires have been hypothesized to select for seedling recruitment after fires (Keeley and Zedler 1978, Malanson 1985, Hilbert 1987). Within a given geographic region, therefore, postfire seedling recruitment should be more prevalent in ecosystems with more infrequent, intense fires.

Site characteristics potentially influence postfire recruitment by constraining species responses to the fire regime and/or by modifying the fire regime itself. Several studies have documented that community characteristics related to postfire seedling establishment vary within regions with differences in water availability. In South African mountain fynbos, for example, relative importance of obligately-seeding species was higher in sites with lower rainfall (Smith et al. 1992), and in Australian sites in Western Australia, South Australia, Victoria, New South Wales and Queensland, biomass of plants regenerating from seeds was higher in drier habitats (Specht 1981). In New Jersey pine barrens, serotinous-coned pitch pines (Pinus rigida) occur on sandy, relatively xeric soils (Whittaker 1979).

Based on the trends discussed above, it appears that within a given region, the potential for postfire seedling recruitment is determined by the soil characteristics and disturbance regime (of disturbances other than fire) under which species traits have evolved. Given the potential for seedling establishment in each region, postfire seedling recruitment within regions appears to be more prevalent in communities in which competition from resprouting adults is relatively low (e.g., communities with intense fires, xeric communities). Thus the importance of postfire seedling recruitment at the community level reflects the role of fire within the abiotic environment in a community.

The objective of this study was to evaluate the role of fire as a disturbance in a southeastern United States fire-influenced ecosystem in comparison with other fire-influenced ecosystems in California. I quantified seedling density and proportion of species represented by seedlings as indices of importance of postfire seedling recruitment; I also quantified abiotic site characteristics. To suggest processes influencing postfire recruitment in different ecosystems and at different spatial scales, I examined trends in seedling recruitment and site characteristics among ecosystems both within and between geographic regions.

A focal ecosystem of the study was sand pine scrub, a pine - scrub oak ecosystem occurring on well-drained, low-nutrient sandy soils primarily in Florida. As in other upland Florida ecosystems, fire is a regular occurrence, especially in sand pine scrub occurring in inland peninsular regions of Florida. Lightning-ignited natural fires occur in inland peninsular sand pine scrub every 10 - 100 years. Although several plant species, such as the serotinous-coned sand pine (Pinus clausa var. clausa; Ward 1963), have seedling recruitment closely linked to fire occurrence, seedling recruitment is completely uncoupled from fire occurrence for many other species such as oaks (Quercus spp.) and scrub hickory (Carya floridana; Myers 1990).

The regions that I compared were inland peninsular Florida and southern California. The regions differ in soil characteristics, climate and fire regime. Upland Florida soils are nutrient-poor entisols (Brown et al. 1990), but southern California soils are relatively nutrient-rich xeralfs (Foth 1978). Florida has a humid climate with primarily summer rainfall, and California has a semi-arid Mediterranean climate. In Florida natural fires occur during wet summers and are followed by relatively dry winters (Myers 1990); in California fires occur during dry summers and are followed by wet winters (Hanes 1991).

I quantified data on seedling recruitment and site characteristics in sand pine scrub and two other Florida ecosystems (i.e., sandhill and rosemary scrub), and in three southern California ecosystems (i.e., chamise chaparral, mixed chaparral and coastal sage scrub) for between- and within-region comparisons. I expected that importance of postfire seedling recruitment would vary between regions with contrasts in abiotic conditions between paired recently burned and mature sites. Because postfire seedling recruitment in many species is presumably a response to good conditions for survival after fires relative to conditions before fires, I expected that postfire seedling recruitment would be most important in the region with the largest fire-induced contrasts in abiotic site characteristics.

I expected within-region trends in postfire seedling recruitment and site characteristics to be different in Florida and California. In Florida's wet climate, seedlings establishing after fires generally face intense competition from quickly-resprouting adult plants; therefore, seedling recruitment should be more successful under conditions of reduced competition. I expected that postfire seedling recruitment in Florida would become more important as surface soils became more xeric and more nutrient-poor. In California's arid climate, however, postfire regrowth of adult plants is relatively slow, and competition should be less intense for seedlings than in Florida. If competition is not a prevailing influence on seedling recruitment, then recruitment should be most successful under conditions of high resource availability. I expected that postfire seedling recruitment in California would become more important as surface soils became more mesic and more nutrient-rich.

Methods

Study Areas

Seedling densities, proportions of species represented by seedlings, and site characteristics were quantified in paired recently burned and mature sites of three community types in Florida and three community types in California. Burned-mature site pairs were replicated five times for each community type.

Florida sites

Florida sites, in rosemary scrub, sand pine scrub and sandhill community types, were located in Ocala National Forest in Marion County, Withlacoochee State Forest in Sumter and Citrus Counties, Tiger Creek and Saddleblanket Lake Preserves in Polk County, and Lake Apthorpe Preserve and Archbold Biological Station in Highlands County (Figure 6-1). Nomenclature for Florida species follows Wunderlin (1982) unless otherwise noted.

Climate, soils and fire season are similar for all Florida community types. Florida has a humid, largely subtropical climate; annual precipitation in the study area is approximately 1400 mm, with 60 - 70% of the precipitation occurring during the summer, from June to October (Chen and Gerber 1990). Sites in all community types have more-or-less flat topography, and occur on well-drained, sandy, low-nutrient soils (Myers 1990); soils are classified as quartzipsamments (Foth 1978).

Rosemary scrub, sand pine scrub and sandhill communities, however, differ in physiognomy, species composition and fire frequency and intensity. Rosemary scrub is shrub-dominated; sand pine (*Pinus clausa*), the only tree species, is sparse if present. The dominant species is Florida rosemary (*Ceratiola ericoides*), a needle-leaved, obligately-seeding shrub. Florida rosemary may occur as a monoculture or with other shrubs such as oaks (*Quercus* spp.) and *Sabal etonia*. Herbaceous species are usually sparse in

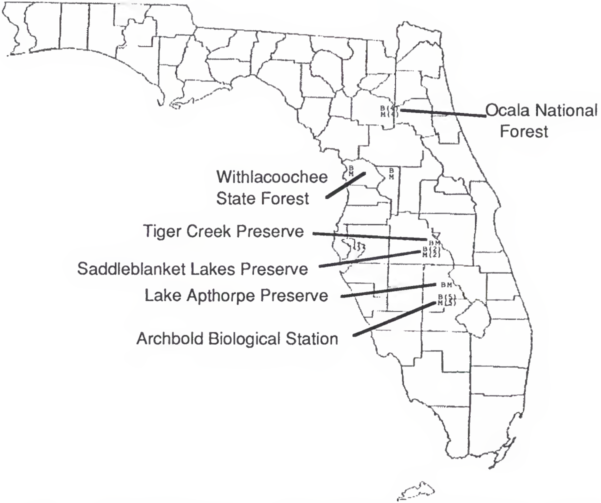


Figure 6-1. Map of study sites in recently burned (B) and mature (M) communities in Florida.

mature sites, and large openings with bare soil may occur between shrubs. Rosemary scrub burns in intense, infrequent fires; fire return intervals are usually at least 30 to 40 years (Myers 1990).

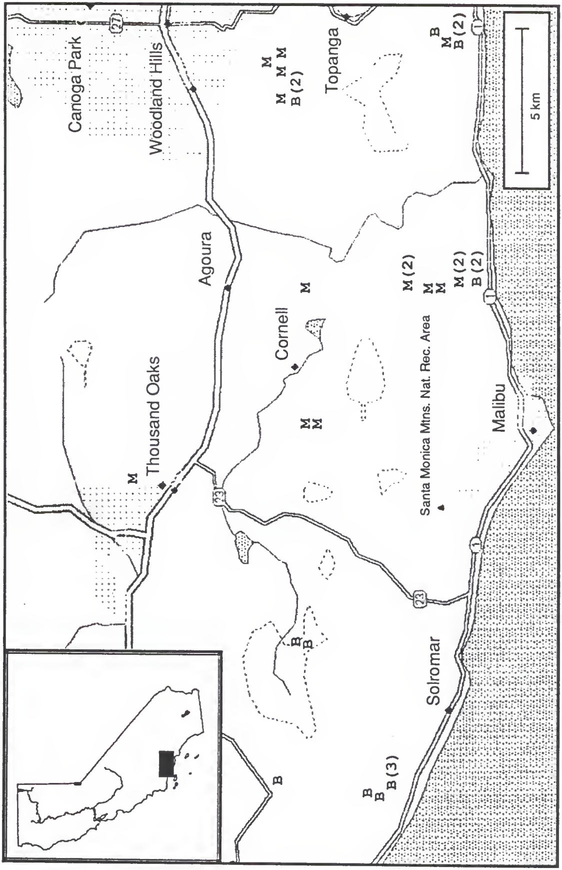
Sand pine scrub, in contrast to rosemary scrub, typically has a high density of shrubs and small trees, with an often dense overstory of sand pines. The understory consists largely of several oak species capable of resprouting after fires; herbaceous species are sparse. Intense fires occur every 10 to 100 years, killing adult sand pines and triggering seed release from cones (Myers 1990).

Sandhill communities typically have a diverse understory of herbaceous species, including many grasses, and an overstory of widely-spaced, fire-resistant longleaf pine (Pinus palustris). Ground cover and litter are often abundant, and the shrub layer of resprouting oaks is usually sparse. Low-intensity ground fires occur every two to ten years (Myers 1990).

California sites

California sites were located from 100 - 600 m elevation in the Santa Monica Mountains in Los Angeles and Ventura Counties, California (Figure 6-2). The climate in this region is Mediterranean, with warm, dry summers and cool, wet winters. Average yearly precipitation is 400 - 600 mm, with approximately 80% of the precipitation

Figure 6-2. Map of study sites in recently burned (B) and mature (M) communities in the Santa Monica Mountains, California.


Canoga Park
Woodland Hills
Topanga
Agoura
Cornell
Thousand Oaks
Santa Monica Mtns. Nat. Rec. Area
Malibu
Solromar
5 km
27
23
1
M
M M M
M M
B(2)
B
M
B(2)
M(2)
M
M
M(2)
B(2)
M
M
M
B
B
B
B
B
B(3)

occurring during the winter (Radtke et al. 1982). Topography is rugged, with 25 - 50% slopes. Soils are largely xerorthents, with some xeralfs occurring in the region (Foth 1978).

Study sites were located in three general community types: (1) chamise chaparral, (2) mixed chaparral and (3) coastal sage scrub. The two chaparral community types share characteristics (e.g., physiognomy, fire frequency, intensity and season) common to all California chaparral, but differ in site characteristics and species composition. Evergreen, sclerophyllous-leaved shrubs 1-6 m tall are dominant in California chaparral, with their intertwining branches typically forming impenetrable thickets. Intense fires occur approximately every 10 to 40 years during the summer dry season (Hanes 1981). Nomenclature for California species follows Hickman (1993).

Chamise chaparral is the predominant chaparral community type in the Santa Monica Mountains. Although chamise chaparral may occur under most site conditions in this region, it is most often on relatively xeric south- and west-facing slopes. The community is dominated by chamise (Adenostoma fasciculatum), a needle-leaved shrub capable of both resprouting and establishing seedlings after fires. Other shrub species such as Salvia mellifera and Eriogonum fasciculatum may co-occur with chamise, but no understory exists and litter is sparse in mature chamise chaparral (Hanes 1981).

Mixed chaparral tends to occur on relatively mesic north- and east-facing slopes in the study area, and is dominated by one or more of several species with various life history characteristics. The most common species include *Ceanothus megacarpus*, an obligately-seeding species, *Ceanothus spinosus*, a species capable of both resprouting and establishing seedlings after fires, and *Quercus dumosa*, a resprouting species that does not establish seedlings after fires. Other occasionally occurring species are *Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Rhus ovata* and *Adenostoma fasciculatum* (Hanes 1981). Understory species are sparse in mature sites.

Coastal sage scrub usually occurs on drier sites at lower elevations than chaparral, and is characterized by summer-deciduous shrubs 1 - 3 m tall. Mature coastal sage scrub is often more open than mature chaparral, and understory herbaceous species are more numerous. Shrub species commonly present include *Artemesia californica*, *Eriogonum fasciculatum*, *Hazardia squarrosus*, and *Salvia leucophylla* (Hanes 1981); most shrub species in coastal sage scrub are capable of resprouting after fires. Fires in coastal sage scrub are often more frequent than in chaparral, and may occur as often as every 5 - 10 years (Keeley and Keeley 1988).

Data Collection

Seedling density and species richness, total species richness and percent open canopy were quantified, and soil samples were collected in all sites. Most data were collected in Florida sites from December 1993 to August 1994; one sand pine scrub burned-mature site pair was studied during July 1995.

Burned and mature sites within Florida communities were paired by location and data collection date. All sites within pairs were less than 1 km apart, and most data collection dates within site pairs differed by six days or less. Exceptions were a sand pine scrub site pair and a rosemary scrub site pair at Archbold Biological Station; data collection dates differed by 151 days between sites in both pairs. All burned sites burned three months to one year before the data collection date.

At each site, seedling density and species and adult plant species composition were quantified within 6, 8 x 1 m randomly located plots. Percent open canopy was quantified with a spherical densiometer (Lemmon 1957) placed on the ground at the midpoints of four randomly selected plots, and a sample of soil was collected to a depth of 5 cm at the midpoints of three randomly selected plots.

Data were collected from California sites from February to June 1994. All burned sites burned during October and November 1993; burned and mature sites within community types were paired by aspect, location and collection date.

Distances between paired sites ranged from 0.5 to 33 km. The median time between collection dates at paired sites was 18 days (range = 1 - 40 days).

In unburned sites, data were collected within 6 randomly located 8 x 1 m plots as in the Florida sites, with plots oriented parallel to slope contour. Data collection methods for the burned sites differed slightly, however. At these sites data were collected within a 50 x 20 m area oriented with the long axis parallel to the slope contour, and subdivided into 10 adjacent 10 x 10 m plots. Seedling density and species and adult plant species composition were quantified within 20, 1 x 1 m plots; two plots were located at opposite corners within each 10 x 10 m plot. Percent open canopy was quantified by placing a spherical densiometer on the ground at four random points within the 50 x 20 m area. Three soil samples were taken at random locations along the outside perimeter of the area; each sample was collected to a depth of 5 cm.

Soil analysis

Percent total nitrogen, total phosphorus, sand and clay, and pH were quantified for each soil sample. Total nitrogen was determined via flash combustion using a Carlos Erba Combustion Analyzer. Percent phosphorus was quantified by digestion with 60% perchloric acid after first digesting the samples with nitric acid to oxidize organic matter (Olsen and Sommers 1982). Percent sand and clay in samples were determined using the hydrometer method for California samples (Cox 1985) and the pipet method for Florida soils (Gee and Bauder 1986). Analysis of four California samples using both methods indicated no difference between the methods.

Data analysis

For each site, seedling density/m^2 was averaged over all plots. Proportion of species represented by seedlings was calculated by dividing number of seedling species in each plot by the total number of species (including seedling species) in the plot. Proportions calculated for all plots then were averaged for each site. Means for percent open canopy and soil phosphorus, nitrogen, sand, clay and pH also were calculated for each site.

Initial statistical analyses were conducted to detect differences in seedling abundance and site characteristics between paired burned and mature sites. Differences between paired sites in seedling density, canopy openness and soil total phosphorus, nitrogen and pH were analyzed using paired t-tests (SAS Institute Inc. 1988).

The remaining analyses were conducted on data from burned sites. First, differences between Florida and California sites in seedling- and site-related variables were analyzed. Differences in seedling density and in seedling proportion were detected using a Kruskal-Wallis test and an analysis of variance, respectively. Stepwise discriminant analysis was used to identify site variables that best discriminated between Florida and California sites (SAS Institute Inc. 1988).

Then ordinations based on site-related variables were conducted using canonical discriminant analyses (SAS Institute Inc. 1988), and relationships between seedling- and site-related variables were analyzed using canonical correlations (SAS Institute Inc. 1988). Canonical discriminant analyses and canonical correlations were conducted separately for Florida and California sites. For each of the two canonical correlations, seedling density and proportion of species represented by seedlings were designated as criterion variables, and percent open canopy and soil phosphorus, nitrogen, sand, clay and pH were designated as predictor variables (Dillon and Goldstein 1984).

Results

Recently burned sites in California tended to have higher numbers of seedling species than in Florida, even though species in California were quantified over a smaller area per site (Table 6-1). Annuals comprised large proportions of the seedling species in California, whereas Florida communities had virtually no annuals among the seedlings (Table 6-2). Seedling densities at the 1 x 1 m scale were lowest in Florida sandhill (median: 2.2 seedlings/m^2; range: 0.2 - 2.7 seedlings/m^2) and highest in California coastal sage scrub (median: 42.4 seedlings/m^2;

Table 6-1. Seedling density, seedling and total species richness, and percent of species represented by seedlings in recently burned Florida rosemary scrub, sand pine scrub and sandhill; and California chamise chaparral, mixed chaparral and coastal sage scrub sites. Data were collected from December 1993 - July 1995, 3 - 12 months after each of the sites burned.

Community Type (n = 5)	Seedlings/m^2† (median (range))	# Seedling Spp.* (mean ± S.E.)	Total # Spp.* (mean ± S.E.)	% of Total Species as Seedlings‡ (mean ± S.E.)
Rosemary Scrub	31.7 (1.4 - 39.9)^{ac}	10.4 ± 1.3	23.8 ± 1.6	43.0 ± 4.4^{ac}
Sand Pine Scrub	3.0 (0.2 - 4.3)^{ad}	7.4 ± 2.0	21.2 ± 3.1	28.8 ± 2.4^{ad}
Sandhill	2.2 (0.2 - 2.7)^{ad}	7.8 ± 1.5	38.8 ± 6.3	18.0 ± 2.1^{ad}
Chamise Chap.	24.0 (6.1 - 41.2)^{b}	14.0 ± 1.8	23.8 ± 4.2	71.4 ± 3.4^{b}
Mixed Chaparral	12.6 (4.7 - 34.7)^{b}	17.2 ± 4.5	27.2 ± 5.3	67.0 ± 6.8^{b}
Coastal Sage	42.4 (6.0 - 214.9)^{b}	11.6 ± 1.1	23.6 ± 3.2	48.8 ± 3.8^{b}

†Superscripts show results of planned contrasts after Kruskal-Wallis test ($p < 0.001$).

*Species were counted over 20 m^2 and 48 m^2 in California and Florida sites, respectively; therefore, differences in means were not tested statistically.

‡Superscripts show results of planned contrasts after ANOVA ($p < 0.001$).

Table 6-2. Numbers of species of seedlings of annuals and perennials in recently burned sites of Florida rosemary scrub, sand pine scrub and sandhill; and California chamise chaparral, mixed chaparral and coastal sage scrub. Species were counted over 20 m^2 and 48 m^2 in California and Florida sites, respectively.

Community Type (n = 5 for each mean)	# Annual Species (mean ± S.E.)	# Perennial Species (mean ± S.E.)
Rosemary scrub	1.4 ± 0.2	9.2 ± 1.4
Sand pine scrub	0.8 ± 0.5	6.6 ± 1.7
Sandhill	0.0 ± 0.0	7.8 ± 1.5
Chamise chaparral	6.2 ± 0.9	6.0 ± 1.3
Mixed chaparral	11.2 ± 3.2	6.0 ± 1.5
Coastal sage scrub	7.4 ± 0.8	3.4 ± 0.4

range: 6.0 - 214.9 seedlings/m^2) and generally were higher in California communities than in Florida communities (Dunn's test, $p < 0.001$; Table 6-1). Total species richness (including adult plants) varied from 21.2 ± 3.1 species in Florida sand pine scrub to 38.8 ± 6.3 species in Florida sandhill. At the 1 x 1 m scale, mean percent of total species represented by seedlings varied from 18.0 ± 2.1% in Florida sandhill to 71.4 ± 3.4% in California chamise chaparral, and was higher in California communities ($F_{1,24}$ = 70.8, $p < 0.001$; Table 6-1).

California and Florida sites were very different with respect to most of the site variables quantified. California soils had higher percent total nitrogen, percent clay and pH, while Florida soils had higher percent sand (stepwise discriminant analysis, $p < 0.05$ for nitrogen, clay and pH; Tables 6-3, 6-4 and 6-5).

Table 6-3. Means (S.E. under each mean) of seedling densities and canopy and soil characteristics quantified from December 1993 - July 1995 in paired burned (B) and unburned (UB) sites of three community types in central Florida. Burned sites burned 3 - 12 months before data collection.

Sites (n = 5 for each mean)	Seedlings/m^2		% Open Canopy		% Total Phosphorus		% Total Nitrogen		pH	
	B	UB	B	UB	B	UB	B	UB	B	UB
Rosemary Scrub	24.1^{*} (7.3)	0.8 (0.5)	73.0^{*} (4.8)	31.9 (7.8)	0.003 (0.001)	0.003 (0.001)	0.023 (0.002)	0.024 (0.005)	4.70^{*} (0.04)	4.53 (0.06)
Sandhill	1.8 (0.4)	0.8 (0.4)	30.5 (4.5)	22.5 (7.2)	0.030 (0.015)	0.022 (0.012)	0.045 (0.005)	0.051 (0.006)	4.40 (0.21)	4.24 (0.26)
Sand Pine Scrub	2.4 (0.8)	0.3 (0.2)	25.5^{**} (3.9)	8.1 (1.6)	0.007 (0.002)	0.010 (0.003)	0.084 (0.020)	0.049 (0.004)	4.17 (0.15)	4.00 (0.11)

*, **Mean difference between B and UB sites was significant (*: $p < 0.05$; **: $p < 0.01$)

Table 6-4. Means (S.E. under each mean) of seedling densities and canopy and soil characteristics quantified from February - June 1994 in paired burned (B) and unburned (UB) sites of chamise chaparral, mixed chaparral and coastal sage scrub in the Santa Monica Mountains in California. Sites burned during October - November 1993.

Sites ($\underline{n}$ = 5 for each mean)	Seedlings/m^2		% Open Canopy		% Total Phosphorus		% Total Nitrogen		pH	
	B	UB	B	UB	B	UB	B	UB	B	UB
Chamise Chaparral	23.9 (5.9)	4.5 (2.5)	78.9** (3.6)	14.6 (5.3)	0.055 (0.003)	0.052 (0.012)	0.323 (0.078)	0.277 (0.068)	6.70 (0.05)	6.42 (0.15)
Mixed Chaparral	15.6 (5.2)	3.8 (3.0)	62.8** (8.8)	7.5 (2.4)	0.049 (0.006)	0.044 (0.002)	0.302 (0.055)	0.259 (0.040)	6.48 (0.12)	6.63 (0.08)
Coastal Sage Scrub	70.6 (38.1)	8.0 (2.1)	67.9** (7.5)	10.1 (2.2)	0.072 (0.007)	0.098 (0.024)	0.293 (0.004)	0.317 (0.022)	6.44 (0.08)	6.22 (0.16)

*, **Mean difference between B and UB sites was significant (*: $\underline{p} < 0.05$; **: $\underline{p} < 0.01$)

Table 6-5. Mean (± S.E.) percent sand and clay in soils of recently burned sites in three Florida communities and three California communities. Community types were rosemary scrub, sand pine scrub and sandhill in Florida; and chamise chaparral, mixed chaparral and coastal sage scrub in California.

Community Type (n = 5 for each mean)	% Sand (mean ± S.E.)	% Clay (mean ± S.E.)
Rosemary scrub	97.1 ± 0.1	0.8 ± 0.1
Sand pine scrub	92.6 ± 1.9	1.0 ± 0.2
Sandhill	93.7 ± 1.1	2.0 ± 0.4
Chamise chaparral	51.6 ± 4.6	19.2 ± 2.3
Mixed chaparral	62.8 ± 2.5	14.3 ± 1.4
Coastal sage scrub	52.0 ± 4.1	23.2 ± 5.5

Differences between Burned and Mature Sites

Seedling and site variables differed among Florida community types. Percent open canopy values were higher in burned than in mature rosemary scrub and sand pine scrub, but did not differ between paired burned and mature sandhill sites. Seedling density and soil pH were higher in burned than mature rosemary scrub sites (Table 6-3). Although seedling densities did not differ within site pairs in sand pine scrub and sandhill, seedling species composition was dissimilar between burned and mature sites. Coefficients of community similarity (Mueller-Dombois and Ellenberg 1974) were 0 and 0.23 for sand pine scrub and sandhill, respectively (Table 6-6). Neither soil phosphorus nor soil nitrogen differed between burned and mature sites in all Florida community types (Table 6-3).

Differences between paired burned and unburned sites were similar in all California community types. Of the variables quantified, only percent open canopy differed between paired burned and mature sites, with burned sites in all site pairs having greater percent open canopy values than mature sites (Table 6-4).

Seedling species were more similar between burned and mature sites in mixed chaparral and coastal sage scrub than in chamise chaparral and communities in Florida (Tables 6-6 and 6-7). Coastal sage scrub had the highest community similarity (coefficient of community similarity = 0.37); however, almost half of the species that occurred in both burned and mature sites were exotics (Table 6-7).

Patterns of Seedling and Site Variables in Burned Sites

Florida sites

The canonical discriminant analysis comparing Florida community types yielded one significant axis that accounted for 80% of the variability in the data (Table 6-8). Rosemary scrub sites, with more open canopies and sandier, higher-pH, lower-nitrogen soils, were clearly separated from sand pine scrub and sandhill sites along the axis. Sand pine scrub sites and sandhill sites were less clearly separated from each other, but sand pine scrub sites tended to have less open canopies, higher soil nitrogen and lower pH than sandhill sites (Figure 6-3).

Table 6-6. Species of seedlings present in recently burned and mature sites of Florida rosemary scrub, sand pine scrub and sandhill. Species were quantified in five sites of each community type during December 1993 - July 1995. Burned sites burned 3 - 12 months before data collection. Letters in parentheses indicate whether seedling species is annual (a) or perennial (p).

	Seedling Species Present in Community Types	
Rosemary Scrub	Sand Pine Scrub	Sandhill
Balduina angustifolia (p)	*Cyperus* spp. (3 species) (p)[a]	*Asclepias verticillata* (p)
Calamintha ashei (p)[a]	*Dicanthelium* sp. (p)[a]	*Balduina angustifolia* (p)[b]
Ceratiola ericoides (p)[a]	*Eupatorium* sp. (p)[a]	*Cassia chamaecrista* (p)[a]
Conradina brevifolia (p)[a]	*Galactia regularis* (p)[a]	*Cassia* sp. (p)[b]
Cyperus spp. (2 species) (p)[a]	*Garberia heterophylla* (p)[a]	*Centrosema* sp. (p)
Galactia regularis (p)	*Gnaphalium* sp. (a)[a]	*Crotalaria purshii* (p)[a]
Gratiola ramosa (a)[b]	*Conyza canadensis* (a)[a]	*Cyperus* sp. (p)[b]
Hypericum cumulicola (p)[a]	*Linaria floridana* (a)[a]	*Dalea feayi* (p)[a]
Lechea deckertii (p)[a]	*Palafoxia feayi* (p)[a]	*Dicanthelium* sp. (p)[a]
Linaria floridana (a)[a]	*Pinus clausa* (p)[a]	*Gnaphalium* sp. (a)
Opuntia humifusa (p)[a]	*Polanisia tenuifolia* (p)[a]	*Palafoxia feayi* (p)[b]
Palafoxia feayi (p)	*Rhynchospora megalocarpa* (p)[a]	*Pinus clausa* (p)[a]
Paronychia chartacea (a)[b]	*Schrankia uncinata* (p)	*Pinus palustris* (p)[a]
Polanisia tenuifolia (p)[a]	*Solanum* sp. (p)[a]	*Stipulicida setacea* (p)[a]
Polygonella gracilis (p)	*Sporobolus* sp. (p)[a]	*Tephrosia chrysophylla* (p)[a]
Polygonella polygama (p)[b]	*Stipulicida setacea* (p)	Fabaceae (2 species) (p)[a]
Polygonella robusta (p)[a]	*Tephrosia chrysophylla* (p)[a]	Poaceae (3 species) (p)[a]
Stillingia sylvatica (p)[a]	Poaceae (p)[a]	unknown (15 morpho species)
Stipulicida setacea (p)[b]	unknown (6 morpho species)	
Stylisma abdita (p)[a]		
Fabaceae (p)		
Poaceae (p)		
unknown (15 morpho species)		

[a] Present in recently burned sites only.
[b] Present in both recently burned and mature sites.

Table 6-7. Species of seedlings present in recently burned and mature sites of chamise chaparral, mixed chaparral and coastal sage scrub in the Santa Monica Mountains in California. Species were quantified in five sites of each community type during February - June 1994. Sites burned during October - November 1993. Letters in parentheses indicate whether seedling species is annual (a) or perennial (p).

Seedling Species Present in Community Types		
Chamise Chaparral	Mixed Chaparral	Coastal Sage Scrub
Adenostoma fasciculatum (p)^{a}	Adenostoma fasciculatum (p)^{a}	Anagallis arvensis (a)^{b*}
Antirrhinum nuttallianum (a)^{a}	Antirrhinum kelloggii (a)^{a}	Apiastrum angustifolium (a)^{a}
Apiastrum angustifolium (a)^{a}	Antirrhinum nuttallianum (a)^{a}	Artemisia californica (p)^{b}
Artemisia californica (p)	Apiastrum angustifolium (a)^{b}	Astragalus sp. (p)^{a}
Bromus arenarius (a)^{a*}	Avena barbata (a)^{a*}	Brassica nigra (a)^{b*}
Bromus madritensis (a)*	Brassica nigra (a)^{a*}	Bromus madritensis (a)^{b*}
Camissonia californica (a)^{b}	Bromus arizonicus (a)^{a}	Centaurea melitensis (a)^{a*}
Ceanothus megacarpus (p)^{a}	Bromus diandrus (a)^{b*}	Cryptantha muricata (a)^{a}
Chaenactis artemisiifolia (a)^{a}	Bromus japonicus (a)^{a*}	Calystegia macrostegia (p)^{a}
Cryptantha microstachys (a)^{a}	Bromus sp. (a)^{b*}	Daucus pusilus (a)^{a}
Cryptantha muricata (a)^{a}	Camissonia californica (a)^{a}	Emmenanthe penduliflora (a)^{a}
Cryptantha sp. (a)^{b}	Ceanothus megacarpus (p)^{a}	Encelia californica (p)
Calystegia macrostegia (p)^{a}	Ceanothus spinosus (p)^{b}	Erodium cicutarium (a)^{b*}
Dicentra ochroleuca (p)^{a}	Chaenactis artemisiifolia (a)^{a}	Erodium moschatum (a)*
Emmenanthe penduliflora (a)^{a}	Chorizanthe sp. (a)^{a}	Eriogonum cinerum (p)^{a}
Encelia californica (p)	Claytonia perfoliata (a)^{b}	Eschscholzia californica (a)^{a}
Erodium cicutarium (a)*	Conyza canadensis (a)^{a}	Eucrypta chrysanthemifolia (a)^{a}
Eriophyllum confertiflorum (p)^{a}	Cryptantha muricata (a)^{a}	Galium aparine (a)^{b}
Eriogonum fasciculatum (p)^{a}	Cryptantha sp. (a)^{b}	Galium nuttallii (p)^{a}
Eucrypta chrysanthemifolia (a)^{b}	Cuscuta californica (p)^{a}	Gnaphalium sp. (p)
Galium nuttallii (p)^{a}	Calystegia macrostegia (p)^{b}	Hazardia squarrosus (p)
Galium aparine (a)	Dendromecon rigida (p)^{a}	Hemizonia fasciculata (a)^{a}
Helianthus gracilentus (p)^{a}	Emmenanthe penduliflora (a)^{a}	Lathyrus vestitus (p)^{b}
Hemizonia fasciculata (a)^{a}	Erodium cicutarium (a)^{a*}	Lotus salsuginosus (a)^{a}
Lotus salsuginosus (a)^{a}	Eriogonum fasciculatum (p)^{a}	Lotus scoparius (p)^{b}
Lotus scoparius (p)^{b}	Eucrypta chrysanthemifolia (a)^{b}	Lupinus bicolor (a)^{a}
Malocothamnus fasciculatus (p)	Galium aparine (a)^{b}	Lupinus hirsutissimus (a)^{a}

Chamise Chaparral	Seedling Species Present in Community Types Mixed Chaparral	Coastal Sage Scrub
Malosma laurina (p)^{a}	*Galium nuttallii* (p)^{a}	*Lupinus sparsiflorus* (a)^{a}
Malocothrix clevelandii (a)^{a}	*Gnaphalium californicum* (p)^{a}	*Lupinus succulentus* (a)^{a}
Melica imperfecta (p)	*Guillenia lasiophylla* (a)^{a}	*Malocothamnus fasciculatus* (p)^{b}
Penstemon centranthifolius (p)^{a}	*Hazardia squarrosus* (p)^{b}	*Malosma laurina* (p)^{b}
Phacelia cicutaria (a)^{a}	*Hirschfeldia incana* (p)^{a*}	*Phacelia cicutaria* (a)^{a}
Phacelia sp. (a)^{b}	*Lotus salsuginosus* (a)^{a}	*Salvia leucophylla* (p)^{b}
Pterostegia drymarioides (a)	*Lotus scoparius* (p)^{b}	*Silybum marianum* (a)*
Rhus ovata (p)^{a}	*Lupinus succulentus* (a)^{a}	*Solanum xanti* (p)^{a}
Ribes speciosa (p)^{a}	*Malosma laurina* (p)^{a}	*Sonchus* sp. (a)*
Salvia mellifera (p)^{a}	*Malocothrix clevelandii* (a)^{a}	*Stylocline gnaphalioides* (a)
Silene multinervia (a)^{a}	*Mentzelia micrantha* (a)^{a}	*Trifolium hirtum* (a)^{b*}
Sonchus asper (a)^{a*}	*Mimulus aurantiacus* (p)^{b}	*Vulpia* sp. (a)*
Stylocline gnaphalioides (a)	*Papaver californicum* (a)^{a}	Fabaceae (1 species)
Trifolium hirtum (a)^{a*}	*Phacelia cicutaria* (a)^{a}	Poaceae (1 species)
Vulpia myuros (a)*	*Phacelia grandiflora* (a)^{a}	unknown (8 morpho species)
Poaceae (2 species)	*Phacelia parryi* (a)^{a}	
unknown (9 morpho species)	*Phacelia* sp. (a)^{b}	
	Pholistoma auritum (a)^{a}	
	Pterostegia drymarioides (a)^{a}	
	Rafinesquia californica (a)^{a}	
	Rhus ovata (p)^{a}	
	Salvia mellifera (p)^{a}	
	Sanicula crassicaulis (p)^{a}	
	Silene laciniata (p)^{a}	
	Solanum xanti (p)^{a}	
	Stellaria media (a)^{a*}	
	Trifolium hirtum (a)^{a*}	
	Venegasia carpesioides (p)^{b}	
	Vulpia myuros (a)^{a*}	
	unknown (17 morpho species)	

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[a] Present in recently burned sites only.
[b] Present in both recently burned and mature sites.
[*] Exotic species.

Table 6-8. Significance tests of canonical axes summarizing variation in site characteristics among Florida rosemary scrub, sand pine scrub and sandhill community types.

Canonical Variate	Likelihood Ratio	Approx. F	Numerator DF	Denominator DF	P
1[a]	0.043	4.47	12	14	0.005
2	0.358	2.86	5	8	0.090

[a] Canonical axis accounted for 80% of variability in the data.

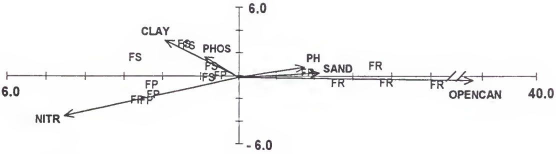

Figure 6-3. The first and second canonical axes from canonical discriminant analysis of recently burned sites in Florida rosemary scrub (FR), sand pine scrub (FP) and sandhill (FS). Coordinates of vectors represent direction and strength of loading on canonical axes for six site variables, and axis lengths are proportional to the amount of variation in site variables that is explained. Site variables are percent open canopy (OPENCAN), percent total soil phosphorus (PHOS), percent total soil nitrogen (NITR), percent sand (SAND), percent clay (CLAY) and soil pH (PH). The first canonical axis explains 80% of the variation in site variables.

Both seedling densities and proportions of species represented by seedlings reflected differences in site characteristics between rosemary scrub and sites in the two other communities; seedling densities and seedling proportions were higher in rosemary scrub sites (Table 6-1). Canonical correlation, however, did not demonstrate significant relationship between seedling and site variables over all of the sites. Neither of the canonical variates was significant (Table 6-9), and both site canonical variates combined explained only 41% of the seedling density and seedling proportion variance.

Table 6-9. Significance tests of canonical variates relating seedling-related variables (i.e., seedling density, proportion of species represented by seedlings) to site-related variables (i.e., percent open canopy and soil phosphorus, nitrogen, sand, clay and pH) in recently burned sites in three inland peninsular Florida communities.

Canonical Variate	Likelihood Ratio	Approx. F	Numerator DF	Denominator DF	P
1	0.274	1.06	12	14	0.453
2	0.608	1.03	5	8	0.459

California sites

The canonical discriminant analysis comparing California community types yielded one significant axis that accounted for 71% of the variability in the data (Table 6-10) and defined a gradient of less open sites with relatively sandy, low-pH soils to more open sites with less sandy, higher-pH soils. Although sites intergraded somewhat, the general order of community types along the gradient was mixed chaparral, coastal sage scrub and chamise chaparral (Figure 6-4).

Although neither seedling densities nor proportions of species represented by seedlings reflected the above-described gradient of site characteristics (Table 6-1), canonical correlation suggested a relationship between seedling-related characteristics of sites (i.e., seedling density, proportion of species represented by seedlings) and site-related characteristics (i.e., percent open canopy and soil phosphorus, nitrogen, sand, clay and pH). The canonical correlation produced two canonical variates, with the first variate significant (Table 6-11). Although the second canonical variate was not significant, it nevertheless substantially improved the canonical correlation of the seedling-related variables with the site-related variables, and is included in the results. The second variate was close to being significant ($\underline{p} = 0.063$; Table 6-11), and both site canonical variates combined explained 78% of the seedling density and seedling proportion variance (Table 6-12).

Seedling density and the proportion of species represented by seedlings were not correlated with each other ($r = -0.17$, $\underline{p} > 0.05$), and were correlated with different canonical variates. The first canonical variate was

Table 6-10. Significance tests of canonical axes summarizing variation in site characteristics among California chamise chaparral, mixed chaparral and coastal sage scrub.

Canonical Axis	Likelihood Ratio	Approx. F	Numerator DF	Denominator DF	P
1[a]	0.083	2.89	12	14	0.031
2	0.393	2.47	5	8	0.123

[a] Canonical axis accounted for 71% of variability in the data.

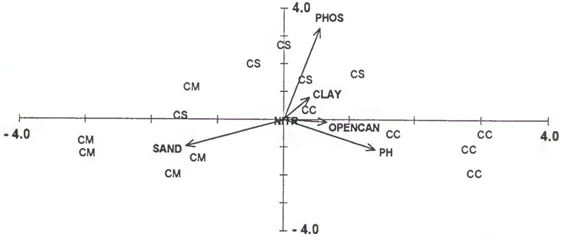

Figure 6-4. The first and second canonical axes from canonical discriminant analysis of recently burned sites in California chamise chaparral (CC), mixed chaparral (CM) and coastal sage scrub (CS). Coordinates of vectors represent direction and strength of loading on canonical axes for six site variables, and axis lengths are proportional to the amount of variation in site variables that is explained. Site variables are percent open canopy (OPENCAN), percent total soil phosphorus (PHOS), percent total soil nitrogen (NITR), percent sand (SAND), percent clay (CLAY) and soil pH (PH). The first canonical axis explains 71% of the variation in site variables.

Table 6-11. Significance tests of canonical variates relating seedling-related variables (i.e., seedling density, proportion of species represented by seedlings) to site-related variables (i.e., percent open canopy and soil phosphorus, nitrogen, sand, clay and pH) in recently burned sites in three southern California communities.

Canonical Variate	Likelihood Ratio	Approx. F	Numerator DF	Denominator DF	P
1	0.044	4.42	12	14	0.005
2	0.323	3.35	5	8	0.063

Table 6-12. Loadings of seedling and site variables from recently burned sites in three southern California communities on canonical variates, and canonical correlations. Seedling-related variables are seedling density (DENSITY) and proportion of species represented by seedlings (PROPSPP); site-related variables are percent open canopy (OPENCAN), percent total soil phosphorus (PHOS), percent total soil nitrogen (NITR), percent soil sand (SAND), percent soil clay (CLAY) and soil pH (PH).

	Canonical Variate	
Variables	1	2
Seedling		
DENSITY	-0.259	0.966
PROPSPP	0.996	0.095
Site		
OPENCAN	-0.182	-0.488
PHOS	-0.526	0.292
NITR	-0.021	-0.016
SAND	0.057	-0.493
CLAY	-0.174	0.803
PH	0.767	0.417
Canonical Correlations	0.898[a]	0.789[b]

[a] Site canonical variables accounted for 46% of DENSITY and PROPSPP variance.

[b] Site canonical variables accounted for 32% of DENSITY and PROPSPP variance.

associated with high seedling proportion values. Of the site-related variables, this canonical variate was associated with high soil pH and low phosphorus. The second canonical variate, associated with high seedling densities, also was associated with high clay contents and low sand and canopy openness values (Table 6-12).

Discussion

Seedling densities, proportions of species represented by seedlings and abiotic characteristics of sites were clearly different between Florida and California community types. Different trends in seedling variables in relation to site variables within regions suggest that different processes control patterns of postfire recruitment in Florida and California communities.

Between-region Comparisons

Comparisons of site characteristics between mature and burned sites across regions partially supported the hypothesis that postfire seedling recruitment becomes more important as mature site vs. burned site contrasts become larger. Paired burned and mature sites in California generally had larger contrasts in percent open canopy than in Florida, and California burned sites had higher seedling densities and proportions of species represented by seedlings. No meaningful between-region trends were present for other site variables, however.

The greater contrasts in canopy openness in California sites were most likely due to higher fire intensities and slower vegetation regrowth after fires. Conditions associated with an open canopy, such as increased light availability, exposed mineral soil, adult plant mortality and reduced competition from adult plants, should be beneficial for postfire seedling establishment. In a recent study quantifying direct and indirect effects of burning on postfire seedling establishment in inland and coastal California chaparral, high postfire seedling densities were associated to varying degrees with shrub removal, herbivore exclusion, and direct effects of burning (e.g., heat, smoke). Although herbivore exclusion consistently increased seedling densities across sites, effects of shrub removal and burning appeared to vary with species composition and rainfall at sites (Tyler 1995).

The trend of increased importance of seedling establishment with greater contrasts in percent open canopy between mature and burned sites was absent among Florida community types. Although sand pine scrub had the highest contrasts in percent open canopy between paired sites, rosemary scrub had the highest values for seedling density and the highest proportions of species represented by seedlings after fire. Percent open canopy was higher in burned rosemary scrub sites than in mature sites, even though the mature sites were more open than mature sites in other Florida community types. The contrast in percent open canopy between burned and mature rosemary scrub was most likely due to slower vegetation regrowth, and should be associated with decreased competition for establishing seedlings. In sandhill, percent open canopy was not different between burned and mature sites, probably due to low-intensity fires. Low adult plant mortality rates associated with low-intensity fires may make postfire seedling establishment difficult.

The only burned vs. mature site contrasts in variables other than canopy openness occurred in Florida rosemary scrub. Burned sites in rosemary scrub had higher seedling densities than unburned sites; virtually no seedlings were present in unburned sites, while burned sites had very high seedling densities. Burned vs. mature site contrasts in seedling density were absent for different reasons among community types in Florida and California. In Florida sand pine scrub and sandhill communities, seedling densities were low in both burned and mature sites. In California, however, seedling densities were almost always high in burned sites, but densities in mature sites occasionally exceeded densities in burned sites. The high variation in seedling densities in California mature sites, the relatively similar seedling species compositions between burned and mature California sites, and the consistently low seedling densities in Florida mature sites suggest that in the absence of fire, conditions for early seedling establishment were occasionally good in California, but rarely good in Florida.

Burned vs. mature site contrasts in soil characteristics were absent in all community types except Florida rosemary scrub; burned rosemary scrub sites had higher soil pH than mature sites. The higher pH may improve soil nutrient conditions for plants by promoting higher rates of ammonification and/or nitrification, and by making phosphorus and some cations more available for uptake (Foth 1978, Rundel 1983).

Apparently, no other studies on the effects of fire on soil nutrients have been conducted in rosemary scrub. Although changes in soil nutrients with time since burning have been investigated in oak scrub in east central Florida, soil nutrients were quantified in the most recently burned site two years after burning, and varied more with depth to the water table than with time since burning (Schmalzer and Hinkle 1987). Studies conducted in sandhill ecosystems in South Carolina and Florida showed that for soil phosphorus and nitrogen, neither total nor available levels changed after burning (McKee 1982, Abrahamson 1984a, Anderson and Menges 1996), as was shown for sandhill total phosphorus and nitrogen in this study. A study conducted in North Carolina, however, indicated a short peak in soil ammonium lasting approximately two months after burning (Christensen 1977). As in sandhill sites in this study, the North Carolina and Florida study showed no change in soil pH with burning (Christensen 1977, Abrahamson 1984a), but soil pH was higher after burning in the South Carolina study (McKee 1982).

Several studies have been conducted in California chamise chaparral on the effects of fire on soil nutrients, with varying results. One study suggested that total percent phosphorus did not change after burning (Rundel 1983), while another showed higher total phosphorus levels in burned sites (Christensen and Muller 1975). The lack of contrast in total nitrogen between burned and mature chamise chaparral sites in this study agrees with results from other studies conducted in chamise chaparral. Total nitrogen levels, however, probably do not reflect levels of nitrogen in forms available to plants. In both of the chamise chaparral studies mentioned above, although total nitrogen did not change with burning, soil ammonium levels were higher in burned sites over a 3 - 12 month period after fire, and soil nitrate levels were higher beginning three months after burning, and continuing until at least 12 months after burning (Christensen and Muller 1975, Rundel 1983). A more recent study showed that both soil ammonium and nitrate levels were higher in a burned site 5 and 18 months postfire (Tyler 1994). In contrast to results from this study on changes in soil pH with burning, other studies conducted in California chaparral have reported increases in soil pH after fire (Christensen and Muller 1975, DeBano et al. 1977).

In the present study, small increases in soil total phosphorus and nitrogen and soil pH may have been present in California sites, but undetectable due to inadequate pairing of burned and mature sites. Due to sizes of the wildfires where burned sites were located, mature sites within site pairs were sometimes far from burned sites. Consequently, since site pairing did not reduce within-pair variation in soil variables, small changes in variables could not be detected.

Within-region Comparisons

Florida sites

Rosemary scrub was the only Florida community type clearly different from other community types in abiotic characteristics, seedling density, and proportion of species represented by seedlings. Abiotic characteristics were not clearly different between sand pine scrub and sandhill sites, and this lack of differentiation probably contributed to the poor correlation of seedling variables with site variables across all community types. Much of the variation in the canonical correlation not explained by site canonical variables probably was variation between sand pine scrub and sandhill sites attributable to factors such as past or historical fire frequencies and intensities, rather than site characteristics.

Although only about one third of the variation in seedling recruitment characteristics among Florida community types was correlated with site characteristics, the detectable patterns support the hypothesis that postfire seedling recruitment becomes more important as surface soils become more xeric and nutrient-poor. Rosemary scrub soils had more sand and less nitrogen than soils of other Florida community types. In humid climates such as in Florida, surface soils with high sand content tend to be xeric; sandy soils also usually have low nitrogen levels due to low rates of fixation and high leaching rates (Brown et al. 1990).

Postfire seedling establishment was most prevalent in rosemary scrub, with the highest seedling densities and proportions of species represented by seedlings compared to sandhill and sand pine scrub. Similar results were reported from another study conducted at Archbold Biological Station, in which plant species life history characteristics were compared between rosemary scrub and scrubby flatwoods, a type of Florida scrub most closely resembling sand pine scrub (Menges and Kohfeldt 1995). Postfire seedling establishment was more important in rosemary scrub than in scrubby flatwoods; however, seedling establishment was detected for 62% of the vascular plant species occurring in rosemary scrub, compared to an average of 43% of species represented by seedlings in this study. Most likely, seedlings were detected for more species than in this study because plants were observed over a wider range of conditions; plant species postfire recovery modes were recorded after fires that occurred over a period of three years.

Xeric, low-nutrient soil surface conditions in rosemary scrub should be harsh for early seedling establishment. The same conditions, however, may reduce competition by slowing regrowth of competitively superior adult plants. Menges and Kohfeldt (1995) suggested a similar mechanism to explain the importance of postfire seedling establishment in rosemary scrub relative to scrubby flatwoods. Although explaining mechanisms behind recruitment patterns in rosemary scrub is beyond the scope of this study, the typical brief (1 - 2 year) peaks in densities of short-lived plants after fires in rosemary scrub are similar to patterns of recruitment in California chaparral.

Patterns in seedling and site variables also showed that Florida sand pine scrub is more similar structurally and functionally to sandhill than to rosemary scrub. Sites in sand pine scrub and sandhill community types had less open canopies, soils with less sand and more clay, and lower seedling densities and seedling species proportions than rosemary scrub sites. This conclusion is supported by a soil study conducted in sand pine scrub and sandhill sites in Ocala National Forest that found no differences in soil characteristics between the two community types, and suggested that physiognomic and plant species differences between sand pine scrub and sandhill are due to different fire regimes (Kalisz and Stone 1984; see also Myers 1985).

California sites

Seedling densities and proportions of species represented by seedlings varied in a complex manner with site characteristics in California community types. Seedling density data indicated an opposite trend to that observed in Florida; postfire recruitment became more important as surface soils became more mesic and higher in nutrients. The proportion of species represented by seedlings, however, was not correlated with seedling density, and varied with site characteristics differently.

High seedling densities were correlated with high clay contents, low sand contents and relatively closed canopies. In arid environments, clay in surface soils increases water-holding capacity, but decreases infiltration to deeper levels (Hausenbuiller 1978). The high soil clay contents and relatively shaded conditions should provide more mesic conditions for early postfire seedling establishment, and should allow seedlings (especially of fast-growing annuals) to establish ahead of resprouting plants by taking advantage of surface soil moisture from early precipitation.

High proportions of species represented by seedlings were associated with high soil pH and low soil phosphorus. Although this association is difficult to explain, soil pH and soil phosphorus levels tended to separate coastal sage scrub sites from chamise and mixed chaparral sites in the canonical discriminant analysis (Figure 6-4). In addition, coastal sage scrub had the lowest means for both proportion of species represented by seedlings, and number of seedling species represented by perennials (Table 6-2). The correlation of seedling proportion with the pH - phosphorus canonical variate probably has a fire regime interpretation; coastal sage scrub typically burns more frequently than either chamise or mixed chaparral. Seedling recruitment of perennial species is probably more successful in chamise and mixed chaparral sites that burn relatively infrequently, and these perennial species contribute to high seedling proportions in the sites.

This study was limited in its ability to detect relationships between postfire seedling recruitment and site characteristics across geographical regions. The limitation was largely due to the failure to find differences between paired burned and mature California sites. Fire-induced changes in soil chemical properties are probably small if present in California chaparral, but may be larger than corresponding changes in Florida.

Alternatively, differences in community-level postfire seedling recruitment characteristics between Florida and California may be due to differences in fire regimes and/or differences in phylogenetic histories of the floras, rather than due to differing levels of fire-induced contrasts in site conditions. This alternative seems unlikely, however, since Florida rosemary scrub, with recruitment characteristics relatively similar to those of California sites, had more contrasting site conditions than other Florida community types.

Additional studies are needed to show possible changes in California soils due to fire. In addition, data collected from fire-influenced communities in additional geographical regions could be used to look for general, potentially more illuminating trends in postfire seedling recruitment and site characteristics between regions.

Patterns in seedling and site variables among Florida sites suggested that reduced competition is more important than benign microsite conditions (e.g., high surface soil water-holding capacity, high soil nutrient levels) for successful seedling recruitment over the long term. In contrast, in California, favorable microsite conditions for seedling establishment promoted high seedling densities. Although competition for water is probably common for postfire seedlings in California chaparral (Tyler 1994), results of this study suggest that competition occurs earlier after fires and is more intense in Florida than in California. Differing fire regimes may have been responsible for a portion of the variation in seedling variables among both Florida and California sites not satisfactorily explained by site characteristics.

Instead of competition, allelopathy may be the primary mechanism responsible for postfire seedling recruitment patterns, especially in Florida rosemary scrub. Allelopathic chemicals produced by adult plants and leached from their leaves into the soil and/or present in decaying litter may inhibit seedling establishment in typically open mature rosemary scrub sites (Richardson and Williamson 1988, Fischer et al. 1994). According to the proposed scenario, fire should greatly reduce concentrations of allelochemicals present by consuming litter and aboveground biomass of adult plants. Although allelopathy has been proposed to explain differences in species composition between scrub and sandhill communities in Florida, and a chemical extract from Florida rosemary (Ceratiola ericoides) leaves has been shown to inhibit germination of some species (Tanrisever et al. 1987, Richardson and Williamson 1988), the relative importance of allelopathy vs. competition in influencing community structure has not been demonstrated.

Researchers have claimed the existence of allelopathy in other ecosystems with nutrient-poor and/or xeric soils, including California chaparral (e.g., Muller et al. 1968). The present study, however, does not indicate that allelopathy is a primary mechanism influencing seedling recruitment patterns in California sites, as seedling densities in mature sites occasionally exceeded densities in recently burned sites.

Because the present study only identified patterns in seedling recruitment and site characteristics that suggest underlying processes, experimental studies are needed to determine the underlying mechanisms. Empirical field research is particularly needed on the effects of competition and allelopathy on postfire seedling establishment, and on the influence of fire regime on characteristics of species- and community-level postfire recruitment. Research in these areas will advance progress toward generalizable theory in fire ecology.

CHAPTER 7

SUMMARY AND CONCLUSIONS

This research evaluated the role of fire in Florida sand pine scrub by characterizing postfire recruitment compared with Mediterranean-climate ecosystems. Results showed that although the direct influence of fire on seed survival and microsite conditions appears similar to that in other ecosystems, postfire recruitment is "uncoupled" (*sensu* Grubb 1988) from fire occurrence relative to recruitment in other ecosystems. An analysis of postfire recruitment characteristics in relation to abiotic site characteristics in Florida and California fire-influenced ecosystems suggested that different underlying processes (e.g., interspecific competition, allelopathy) influence patterns of postfire recruitment in different geographic regions.

Effects of Fire on Seed Survival and Seedling Microsites

At the spatial scale of microsites for seedling establishment (i.e. the soil surface to 2 - 3 cm above ground), Florida sand pine scrub is a matrix of light-obscuring shrubs underlain with moderate amounts of litter, interspersed with relatively open areas with little or no litter. In the mature sand pine scrub sites used in this study, most of the scarce seedlings and adult herbaceous and small-statured (< 2 m tall) woody plants occurred in openings (Chapter 2).

Soil Temperatures during Fires

The experimental fires in this study generated extremely high and variable temperatures at the soil surface (Chapter 3), as reported in other fire-influenced ecosystems (e.g., Hobbs et al. 1984, Stott 1986). Temperatures during the fires at the soil surface were almost universally lethal to seeds. Seeds were recovered uncharred in only 3% of the soil surface microsites, and most of the soil surface temperatures were above lethal temperatures documented in this study for seeds of sand pine species, and documented in studies conducted on species in other fire-influenced ecosystems (e.g., Auld and O'Connell 1991). Survival through fire was much more likely for seeds 2 cm or more below the soil surface, where lethal temperatures rarely occurred (Chapter 3).

Effects of Fires on Potential Seedling Microsites

Although the experimental fires strongly affected potential microsites for seedlings by reducing litter depths and increasing canopy openness, spatial patterns of litter depths were largely maintained. After the fires, more seedlings occurred in microsites with less litter (Chapter 2).

Effects of Experimental Microsites on Seedling Establishment

Experiments were conducted to evaluate the effects of pre- and postfire microsite conditions on seedling establishment in the context of Florida sand pine scrub soil and climatic conditions (Chapter 4). Seedling establishment was quantified in experimental microsites simulating pre- and postfire conditions for two representative sand pine scrub species, during the seasons of year in which seedling establishment typically occurred for the species. Experiments were conducted using seeds of *Eriogonum longifolium* var. *gnaphifolium* (Polygonaceae; Reveal 1981) and *Garberia heterophylla* (Asteraceae) during late summer and during late winter - early spring, respectively.

Seedling establishment was water-limited for both species, during both seasons of the year. In addition, results suggested that abiotic microsite conditions for seedling establishment are particularly harsh during summers following growing-season fires. Not only was *Eriogonum* seedling establishment moisture-limited during the relatively wet summer season, but seedlings established only in shaded microsites. Lack of seedling establishment in open microsites typical of postfire conditions may have been due to light-inhibited seed germination (Bewley and Black 1994), or a combination of light inhibition and adverse effects of high soil temperatures on seeds. Harsh postfire conditions for seedling establishment due to high soil temperatures or unfavorable soil moisture conditions also have been documented in sclerophyll shrublands in southwestern Australia and in California chaparral (Keeley and Zedler 1978, Frazer and Davis 1988, Enright and Lamont 1989, Lamont et al. 1993).

Postfire Recruitment Characteristics

Postfire recruitment was characterized in Florida sand pine scrub at the community and species levels, both quantitatively and qualitatively. When compared with Mediterranean-climate ecosystems, postfire recruitment in Florida sand pine scrub appeared relatively uncoupled to fire occurrence (Chapters 2, 5, 6).

Community-level Recruitment Characteristics

Community-level postfire recruitment was characterized by estimating postfire seedling densities and densities of seeds in soil seed banks. Postfire seedling densities in sand pine scrub tended to be low relative to densities reported from other ecosystems (Chapter 2), and the density of seeds in soil seed banks was much lower than seed bank densities reported from California chaparral (Table 5-5).

Community-level postfire recruitment was characterized more qualitatively by evaluating the proportions of species in sand pine scrub with various postfire recruitment traits and growth forms, relative to other ecosystems. Postfire seedling establishment was documented for only 51% of species in the experimentally-burned sand pine scrub sites;

this percentage is similar to 57% of species reported with postfire seedling establishment in Florida scrubby flatwoods (Menges and Kohfeldt 1995). In comparison, postfire seedling establishment has been reported for 90% and 79% of species in California chaparral and Australian heath, respectively (Specht et al. 1958, Vogl and Schorr 1972; Table 2-7). In Florida sand pine scrub, a large proportion of species present both aboveground and in the seed bank was represented by perennials, and annual species were virtually absent. In contrast, in California chaparral annual species comprised a large proportion of species present in seed banks, and of species present aboveground after fires (Vogl and Schorr 1972, Zammit and Zedler 1994; Tables 2-7 and 5-5).

Species-level Recruitment Characteristics

Postfire recruitment traits were characterized for Calamintha ashei (Lamiaceae), Chapmannia floridana (Fabaceae), Eriogonum longifolium var. gnaphifolium (Polygonaceae), Garberia heterophylla (Asteraceae) and Palafoxia feayi (Asteraceae), all small-statured species relatively common in sand pine scrub. These species had a variety of recruitment traits. Chapmannia and Palafoxia resprouted after fire, but had either no or sparse postfire seedling establishment. Calamintha, Eriogonum and Garberia had postfire seedling establishment. Calamintha seedlings presumably originated from seeds in a soil seed bank after adults were killed by fire. In contrast, Eriogonum and Garberia seedlings originated from seeds produced by resprouting, flowering adults. These results suggest that although much of the postfire seedling establishment response in Florida sand pine scrub comes from small-statured herbaceous and woody species (Chapter 2), postfire recruitment traits vary within this general group of species.

Postfire Recruitment Characteristics and Site Characteristics in Florida and California Communities

Postfire recruitment characteristics and site characteristics were compared among Florida and California fire-influenced communities to satisfy two objectives. The first objective was to evaluate the role of fire as a disturbance in Florida sand pine scrub relative to other Florida communities and to fire-influenced communities in southern California. The second objective was to suggest different processes influencing postfire recruitment within the two geographic regions. Communities studied were rosemary scrub, sand pine scrub and sandhill in Florida, and chamise chaparral, mixed chaparral and coastal sage scrub in California (Chapter 6).

California communities, occurring on soils with higher nitrogen levels, higher clay contents, lower sand contents and higher pH than Florida soils, had higher postfire seedling densities and proportions of species represented by seedlings than Florida communities. This more prevalent postfire seedling recruitment in California was associated with greater contrasts between recently burned sites and mature sites in percent open canopy in California than in Florida.

Different trends in seedling recruitment characteristics in relation to site characteristics in recently burned sites within the two geographic regions suggest that different processes control patterns of postfire recruitment in Florida and California communities. In Florida, higher seedling densities and proportions of species represented by seedlings occurred in rosemary scrub, with relatively xeric, nutrient-poor soils. These results at first seem counterintuitive, since the experiments on seedling establishment in experimental microsites demonstrated that seedling establishment is water-limited, and the finer-textured surface soils of sand pine scrub and sandhill sites should provide more mesic conditions for seedling establishment than rosemary scrub soils. Under conditions of intense competition typical in communities in Florida and in other areas with humid climates, however, the same conditions in rosemary scrub that are harsh for seedling establishment may slow the postfire regrowth of potential competitors with seedlings, and may allow more individuals surviving early seedling establishment to reach adulthood.

Among Florida communities, therefore, the association of more prevalent seedling recruitment with more xeric, nutrient-poor soils suggests that reduced competition is more important than favorable microsite conditions for successful seedling recruitment. The importance of reduced competition has been used to explain similar trends of increased seedling recruitment with more xeric conditions in other fire-influenced ecosystems (Specht 1981, Smith et al. 1992).

In contrast with Florida communities, in California high seedling densities occurred in sites with relatively mesic, nutrient-rich soils. This trend suggests that postfire competition is not as intense for seedlings in California as it is for seedlings in Florida.

Postfire regrowth of adult plants is relatively slow in southern California's arid climate. In addition, while the clayey surface soils associated with high seedling densities provide relatively mesic conditions for seedling establishment, they also may reduce infiltration of water and further slow regrowth of adult plants. Such soil conditions should allow seedlings (especially of fast-growing annuals) to establish ahead of resprouting plants by taking advantage of surface soil moisture from early precipitation.

Several researchers have suggested that allelopathy is an important mechanism influencing patterns of seedling establishment in Florida scrub (Richardson and Williamson 1988, Fischer et al. 1994) and in California chaparral (Muller 1968). According to proponents, some chemicals that deter herbivores, and that are typically produced by plants in xeric and/or nutrient-poor environments, are also allelopathic to other plants and inhibit seedling establishment of some species. Fires, by consuming litter and aboveground plant biomass and by heating the soil, reduce concentrations of allelochemicals in the soil and litter and facilitate seedling establishment. Patterns of seedling densities in rosemary scrub are consistent with allelopathy playing a major role; seedling densities are high after fires, but are low in the absence of fires, even though mature sites typically have open canopies. Patterns of seedling densities in sand pine scrub and sandhill, however, are not consistent with allelopathy; seedling densities are low in both recently burned and mature sites. Although identification of mechanisms underlying seedling recruitment patterns is beyond the scope of this research, variation in belowground competition for water seems a more parsimonious mechanism to explain patterns of seedling densities in all three Florida communities.

Factors Contributing to Postfire Recruitment Characteristics of Communities

In this research, the role of fire in ecosystems was assessed by evaluating the importance of postfire seedling recruitment, as defined by seedling density and proportion of species represented by seedlings. The primary hypothesis proposed for explaining between-region differences in postfire recruitment characteristics was that importance of postfire seedling recruitment increases as fire-induced contrasts in abiotic site conditions become larger. This hypothesis was based on the assumption that postfire seedling recruitment evolves in response to good conditions for seedling survival after fires relative to conditions before fires.

Evolutionary History

Although community characteristics are shaped by evolution of species traits in response to selective pressures (e.g., fire regime characteristics, abiotic site characteristics), evolutionary history and phylogenetic constraints of species influence the trajectory of evolution (Peet 1978, Herrera 1992). Consequently, in species in biogeographically distinct regions, different traits may have evolved in response to similar selective pressures.

An obvious difference between the Florida and southern California communities studied in this dissertation is the abundance of annual species in California communities compared to the scarcity of annual species in Florida communities. I suggest that annuals are virtually absent in Florida pyrogenic communities because the annual life history strategy is generally inviable under the conditions of intense competition and low resource availability (e.g., droughty, nutrient-poor soils) in Florida.

An alternative explanation for the abundance of annuals in California and their scarcity in Florida is based on different evolutionary histories of the communities. Climatic conditions and floras in Florida and California communities were similar early in their evolutionary histories, but diverged markedly during the Quaternary. The sclerophyllous vegetation that characterizes communities in both regions presumably originated as part of the Madro-Tertiary geoflora during the early Tertiary (Axelrod 1958), and floras in both regions initially occurred in temperate climates with adequate summer rainfall (Axelrod 1973, Webb 1990).

The Quaternary in southern California marked the beginning of the Mediterranean climate and regular occurrence of fires, and also has been a period of intense mountain building and regional uplift (Axelrod 1973, 1989). The Mediterranean climate was not constant during the Pleistocene, however, but occurred intermittently during interglacial ages, alternating with wetter, summer-rainfall climates during times of glaciation. The constantly changing landforms, exposed soils and climate provided numerous opportunities for speciation during the Quaternary. The rapid speciation that occurred during this period gave rise to the large number of annual species present in chaparral today (Axelrod 1973).

In contrast, Florida is and always was an area of very low topographic relief. During the Quaternary most of the region alternated between being dry land and sea bottom. During glacial ages sea levels were low; more of Florida was exposed, and the climate was relatively dry. During interglacials parts of the land mass were inundated, and the climate was relatively wet (Webb 1990). Although fluctuating sea levels and resulting changes in land masses probably provided some opportunities for speciation, conditions were much less diverse and less favorable for speciation than in California.

Even if annual species are disregarded and the California and Florida communities considered in this research are compared, however, species with postfire seedling establishment are still better represented among perennial species in California than in Florida. This comparison provides some support for the hypothesis that postfire recruitment characteristics are largely influenced by recent selective pressures (e.g., fire, abiotic site characteristics), because perennial species in California chaparral and Florida scrub have relatively similar evolutionary histories, compared to annual species (Axelrod 1958).

Fire Regime

The fire regime, that presumably has influenced the evolution of species traits in Florida and in southern California, differs between the regions. The major difference in fire regime is fire season. In Florida, natural fires typically occur during the hot wet season, followed by a cool dry season. In California, however, fires typically occur during the hot dry season, followed by a cool wet season.

These differences in fire season may intensify differences between the regions in abiotic and competitive environments for postfire seedling establishment. After fires during the hot wet season in Florida, soil water is available for rapid resprouting of adult plants, and high soil temperatures and rates of evaporation from the soil make abiotic conditions potentially harsh for seedling establishment.

Most postfire seedling establishment in Florida communities occurs during the winters following fires (Whelan 1985, Chapter 2). Although lower air and soil temperatures are more conducive to seedling establishment, overall conditions still may not be very favorable. Seeds are potentially vulnerable to predators while germination is delayed, soil water availability can be low during the winter, seedlings are vulnerable to occasional frosts, and competition and/or allelopathic effects are potentially intense from adult plants that have resprouted.

In southern California communities, seedling establishment also occurs mainly during winters following fires. Abiotic and competitive conditions for seedling establishment, however, are potentially better during winters in California than in Florida. High water availability in surface soils from early winter rains, and low rates of evaporation provide relatively good conditions for seedling establishment. In addition, because of slow water infiltration into dry subsurface soils, resprouting of adult plants may be slow.

Thus fire season, associated with the Mediterranean climate in California, makes possible relatively good abiotic and competitive conditions for seedling establishment. If seedling establishment is more consistently successful in California, then postfire seedling establishment may be more evolutionarily advantageous for species in California than in Florida.

Postfire recruitment characteristics of Arizona chaparral seem to support the idea that postfire seedling establishment is more evolutionarily advantageous in a Mediterranean climate. Arizona chaparral is physiognomically similar to, and shares many taxa with California chaparral, but occurs in an area with summer rainfall. In contrast to California chaparral, most species in Arizona chaparral reportedly resprout after fires (Wright and Bailey 1982).

Research Needed

In this dissertation I documented that postfire seedling recruitment is less prevalent in Florida sand pine scrub than in California chaparral and some other Mediterranean-climate ecosystems. Results also suggest that differences in postfire competitive environments for seedlings underlie differences in postfire recruitment characteristics between Florida and southern California communities.

Although general postfire recruitment traits now are known for most vascular plant species in Florida sand pine scrub (Abrahamson 1984b, Menges and Kohfeldt 1995, Chapter 2), research is needed on seed and germination characteristics (i.e., seed dormancy, seed longevity, germination cues, survival through fires) for many small-statured species. More research linking seed and seedling traits of species with abiotic effects of fires also is needed. This research should include work on detailed spatial patterns of temperatures at the soil surface and below the surface, in conjunction with experiments testing germination of seeds after fires, and from varying depths in the soil.

Patterns in seedling recruitment and site characteristics identified in this research suggested that competition during postfire seedling establishment varies in intensity among communities, and between geographical regions. Studies addressing dynamics of interspecific competition are needed to quantify effects of competition on success of seedling establishment, and to determine underlying mechanisms.

Finally, more research should be conducted comparing postfire recruitment characteristics among fire-influenced communities with relatively similar evolutionary histories. Isolation of effects of factors such as fire regime and climate on evolution of species recruitment traits will contribute to construction of generalizable theory in fire ecology.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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